# A ZOOGEOGRAPHIC ANALYSIS OF THE FISHES OF THE FAMILY MYCTOPHIDAE (OSTEICHTHYES, MYCTOPHIFORMES) FROM THE 1979–SARGASSO SEA EXPEDITION OF R.V. *ANTON DOHRN*

By

P. Alexander Hulley
*South African Museum, Cape Town*

&

Gerhard Krefft
*formerly Institut für Seefischerei der Bundesforschungsanstalt für Fischerei, Hamburg*

(With 22 figures and 12 tables)

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## ABSTRACT

During the second leg of the 1979–Sargasso Sea Expedition, R.V. *Anton Dohrn* occupied a series of stations running south-east of Bermuda to about 25°N and then north-eastwards to the mouth of the English Channel. The MT–1600 and IKMT myctophid samples are analysed independently, using abundances and employing the Bray-Curtis similarity measure with group-average sorting and multi-dimensional scaling ordination. The analyses suggest that for the temperate and subtropical regions of the North Atlantic Ocean, the regional system proposed by Backus *et al.* (1977) is basically accurate, but that the division into North and South Sargasso Sea Provinces requires greater scrutiny, particularly with regard to depth. Indicator species are extracted from the data by the application of information statistic tests. These allow for some comment on community structuring in the geographic regions covered by the transect. The South Sargasso Sea Province is distinguished from the North Sargasso Sea Province by differences in species abundances rather than by differences in faunal structure. The distribution patterns of *Electrona risso, Hygophum benoiti, Benthosema glaciale*, and *Lampanyctus crocodilus* are discussed, those of the latter two species in more detail. It appears that various intraspecific changes do occur across boundary zones, so that the interpretation of these changes should be of prime concern in future investigations of distribution. In conclusion, when catch data are compared with described patterns and subpatterns of distribution, the general rule that species diversity decreases with increasing latitude and that larger populations occur in cold-water species than in warm-water species is confirmed.

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## INTRODUCTION

Recent investigations of Atlantic mesopelagic ichthyogeography have culminated in a series of distributional analyses by Parin *et al.* (1974), Krefft (1974, 1978), and Hulley (1981). A system of zoogeographic regions and provinces has been proposed by Backus *et al.* (1977), whose method is based on the conformance of distribution patterns of individual species to selected oceanic physical boundaries.

The aims of this paper are threefold: firstly, to attempt to assess the accuracy of the faunal region and province system, as proposed by Backus *et al.* (1977), in the subtropical-temperate North Atlantic, using the Myctophidae and a method based on abundances; secondly, to examine some of the nuances of myctophid intraspecific change at boundary zones, which may help to justify this system; and thirdly, to hone current ideas on the problematic distribution patterns of some lanternfish species.

## MATERIALS AND METHODS

The data used in this analysis are the Myctophidae collected by the R.V. *Anton Dohrn* during the 1979–Sargasso Sea Expedition. The primary objective of this expedition was to investigate aspects of the distribution and biology of eels. The stations occupied are given in Figure 1. During the first leg of the expedition, about 5 000 lanternfish specimens were obtained from the stepped MT–1600, IKMT and MOCNESS hauls (stations AD 23/79 through AD 256/79). The area sampled lay mainly to the south-south-east of Bermuda. The second leg (stations AD 268/79 through 401/79) yielded 15 494 lanternfishes from an MT–1600 transect and 1 715 specimens from IKMT stations, which were occupied during the same transect. The transect ran south-east from Bermuda to about 25°N and then in a north-easterly direction towards the southern entrance of the English Channel (Fig. 1). All material was identified, counted and measured at sea, and representative collections are now housed in the following institutions:

Institut für Seefischerei, Zoologisches Museum, Hamburg (ISH)
Muséum National d'Histoire Naturelle, Paris
National Museum of Natural History, Smithsonian Institution, Washington
South African Museum, Cape Town
Zoologisk Museum, Copenhagen

In addition, data from a series of synoptic neuston tows have been examined (H.-C. John, Zoologisches Museum, Hamburg, pers. comm.).

A description of the XBT sections has been given by Wegner (1979) and the temperature section is reproduced as Figure 12. The hydrographic features for some second-leg stations, AD 265/79 through AD 303/79, are included in the descriptions of the Sargasso Sea in spring 1979 (Wegner 1982).

Data only from the second leg have been used for zoogeographic analysis because of the more extensive area sampled during the transect. Further, since

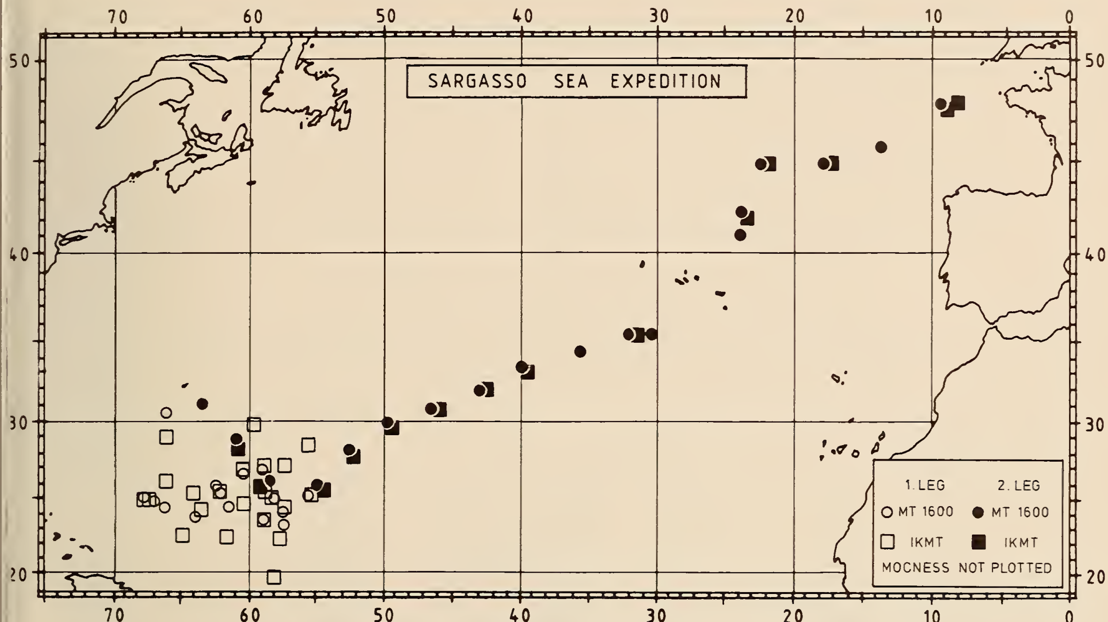


Fig. 1. Station positions for MT–1600 and IKMT hauls for first and second legs of the 1979–Sargasso Sea Expedition of R.V. *Anton Dohrn*. (Note: The 14 IKMT stations from the second leg of the transect are symbolized in this figure; due to the close proximity of certain stations, only 18 of the 38 MT–1600 stations from this leg are depicted; relevant station data are given in Tables 1 and 2.)

both an MT–1600 and an IKMT were deployed, data sets from the two sampling methods could be tested independently. A data matrix of 63 species at 38 stations resulted from the MT–1600 samples, and a data matrix of 33 species at 14 stations from the IKMT samples.

The strategy for analysing marine biological survey data described by Field *et al.* (1982) was used. The methodology is only briefly described below, so that the reader should refer to Field *et al.* (1982) for full details. The advantage of the method is that biotic data are analysed completely separately from environmental data, thereby avoiding any previous assumptions about relationships between biota and environment, cf. Backus *et al.* (1977). The method allows for normal or 'q'-type analysis, in which stations are arranged into groups, each having a similar biotic composition, and inverse or 'r'-type analysis, in which the species are grouped. Further, the application of the information statistic (*I*-) tests to the data matrix provides a means for the recognition of indicator species (Fig. 2).

In the case of the MT–1600 samples, the raw data matrix was scaled to achieve the number of specimens of each species in each haul (station) for a standard period of one hour at fishing depth. The relationship between the computer-generated station numbers and the R.V. *Anton Dohrn* MT–1600

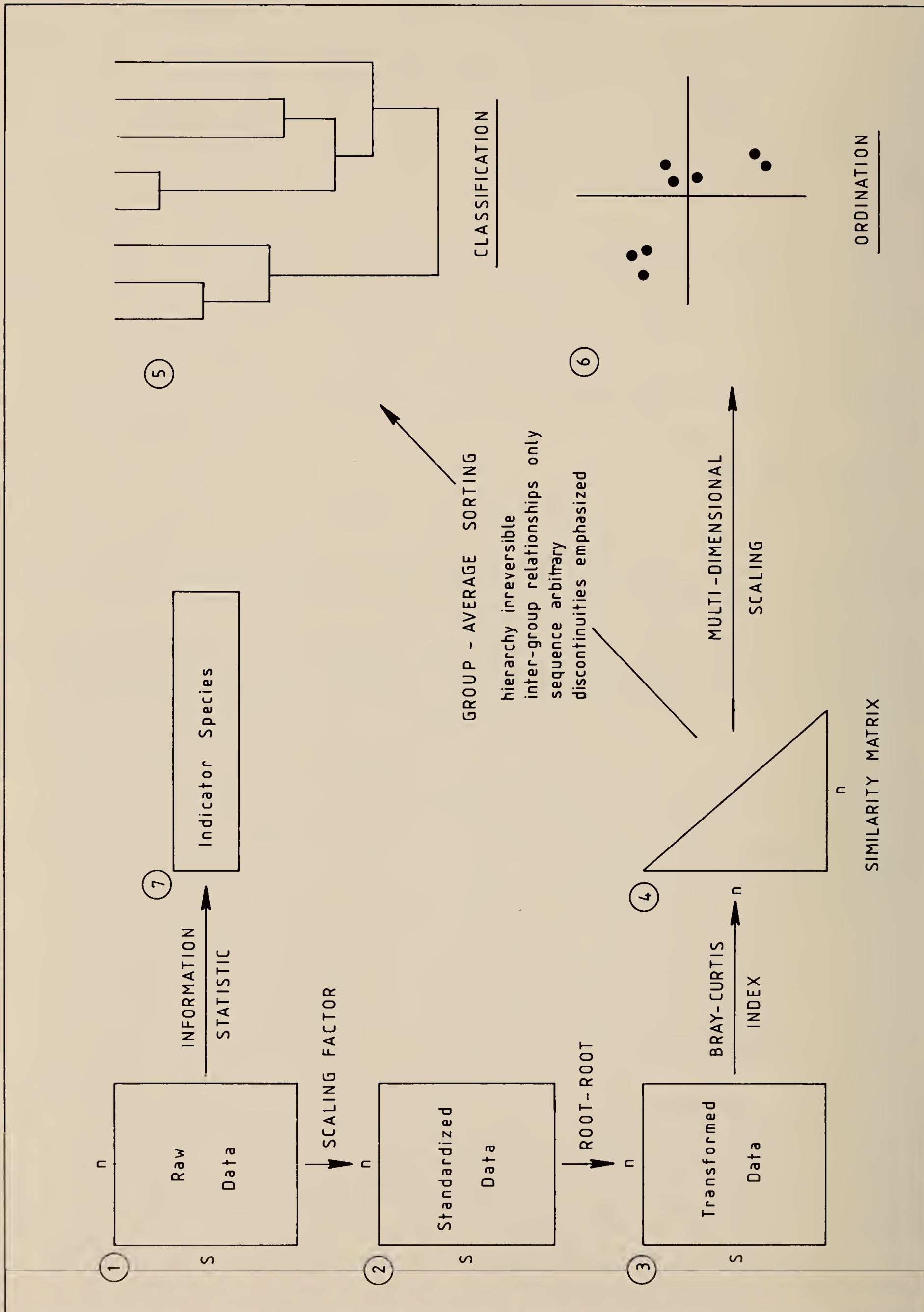


Fig. 2. Flow chart for the Field *et al.* (1982) method of analysis of biological survey data, including disadvantages of group-average sorting.

station numbers is given in Table 1. Since density data are apparently often skewed, in that the abundant species swamp the other data (Field *et al.* 1982), the matrix was root-root transformed. Although the raw data matrix from the IKMT samples was similarly transformed, no scaling factors were employed, because each haul was fished for a standard time and to a similar depth.

The transformed data were then subjected to similarity analysis using the Bray-Curtis measure, resulting in a triangular similarity matrix, whose entries compare each of the samples with every other sample. The technique used to

TABLE 1

1979–Sargasso Sea Expedition (2nd leg). Station list of MT–1600 hauls indicating computer-generated station numbers and their equivalent R.V. *Anton Dohrn* station numbers.

| *Computer station no.* | *AD station no.* | *Position* | | *Date* | *Depth* (m) | *Time at depth* |
|---|---|---|---|---|---|---|
| 1 | 268/79 | 31°11′N | 63°27′W | 19.04.79 | *c.* 1 700 | 1510–1555 |
| 2 | 269/79 | 30°05′N | 63°23′W | 19.04.79 | 170 | 1944–1959 |
| 3 | 270/79 | 31°01′N | 63°15′W | 19.04.79 | 250 | 2055–2110 |
| 4 | 276/79 | 28°41′N | 60°54′W | 20.04.79 | *c.* 1 800 | 1510–1600 |
| 5 | 284/79 | 26°11′N | 58°26′W | 21.04.79 | 2 000 | 1500–1600 |
| 6 | 293/79 | 25°49′N | 54°58′W | 22.04.79 | *c.* 2 000 | 1505–1600 |
| 7 | 301/79 | 27°38′N | 52°22′W | 23.04.79 | 2 000 | 1455–1545 |
| 8 | 302-I/79 | 27°49′N | 52°13′W | 23.04.79 | 300 | 1915–1928 |
| 9 | 308/79 | 29°40′N | 49°38′W | 24.04.79 | *c.* 2 000 | 1535–1630 |
| 10 | 309-I/79 | 29°41′N | 49°27′W | 24.04.79 | 110 | 1917–1932 |
| 11 | 314-I/79 | 30°43′N | 46°16′W | 25.04.79 | 2 000 | 1637–1735 |
| 12 | 314-II/79 | 30°45′N | 46°08′W | 25.04.79 | 195 | 2015–2030 |
| 13 | 315/79 | 30°47′N | 46°04′W | 25.04.79 | 306 | 2110–2125 |
| 14 | 321/79 | 31°51′N | 42°55′W | 26.04.79 | 1 950 | 1630–1725 |
| 15 | 322/79 | 31°53′N | 42°48′W | 26.04.79 | 190 | 2002–2017 |
| 16 | 323/79 | 31°55′N | 42°46′W | 26.04.79 | 380 | 2057–2112 |
| 17 | 329/79 | 32°59′N | 39°41′W | 27.04.79 | 1 950 | 1535–1630 |
| 18 | 330/79 | 33°01′N | 39°34′W | 27.04.79 | 185 | 1955–2010 |
| 19 | 331/79 | 33°04′N | 39°29′W | 27.04.79 | 345 | 2050–2110 |
| 20 | 338/79 | 34°21′N | 35°29′W | 28.04.79 | 1 300 | 1700–1800 |
| 21 | 339/79 | 34°20′N | 35°24′W | 28.04.79 | 170 | 2040–2055 |
| 22 | 340/79 | 34°21′N | 35°22′W | 28.04.79 | 320 | 2133–2148 |
| 23 | 345/79 | 35°24′N | 32°01′W | 29.04.79 | 1 800 | 1700–1750 |
| 24 | 346-I/79 | 35°24′N | 31°53′W | 29.04.79 | 350 | 2030–2045 |
| 25 | 348/79 | 35°20′N | 30°16′W | 30.04.79 | *c.* 1 900 | 0640–0710 |
| 26 | 361/79 | 41°02′N | 23°52′W | 02.05.79 | >2 000 | 1135–1230 |
| 27 | 364/79 | 42°05′N | 23°30′W | 02.05.79 | 155 | 2020–2035 |
| 28 | 365/79 | 42°06′N | 23°29′W | 02.05.79 | 340 | 2110–2125 |
| 29 | 371/79 | 44°54′N | 22°16′W | 03.05.79 | 2 000 | 1638–1730 |
| 30 | 372/79 | 44°56′N | 22°00′W | 03.05.79 | 175 | 2022–2037 |
| 31 | 373/79 | 44°56′N | 21°57′W | 03.05.79 | 340 | 2113–2128 |
| 32 | 380/79 | 44°55′N | 17°34′W | 04.05.79 | 2 000 | 1720–1820 |
| 33 | 381/79 | 44°55′N | 17°22′W | 04.05.79 | 205 | 2100–2115 |
| 34 | 382/79 | 44°56′N | 17°18′W | 04.05.79 | *c.* 350 | 2204–2219 |
| 35 | 389/79 | 45°41′N | 13°42′W | 05.05.79 | *c.* 2 000 | 1713–1810 |
| 36 | 390/79 | 45°54′N | 13°30′W | 05.05.79 | 205 | 2044–2059 |
| 37 | 391/79 | 45°55′N | 13°27′W | 05.05.79 | 350 | 2136–2151 |
| 38 | 398/79 | 47°42′N | 09°08′W | 06.05.79 | 2 000 | 1837–2000 |

produce the dendrogram from the similarity matrix was group-average sorting, which joins two groups of samples together at the average level of similarity between all members of one group and all members of the other.

While dendrograms have the advantage of simplicity, they have a number of disadvantages (*fide* Fig. 2), so that a multi-dimensional scaling (MDS) method of ordination was also employed. This seeks to reconcile the interstation distances in a specified number of dimensions in ordinary Euclidean space, with the physical distances between points on a two-dimensional map.

## RESULTS AND DISCUSSION

*Normal ('q'-type) analysis*

The dendrogram given in Figure 3 shows station affinities based on the root-root transformed abundances of all 63 species of Myctophidae taken during the MT–1600 transect. The broken line drawn at the arbitrary similarity level of 20 per cent delineates two major groups of stations, while the broken line drawn at the arbitrary similarity level of 40 per cent delimits three groups of stations:

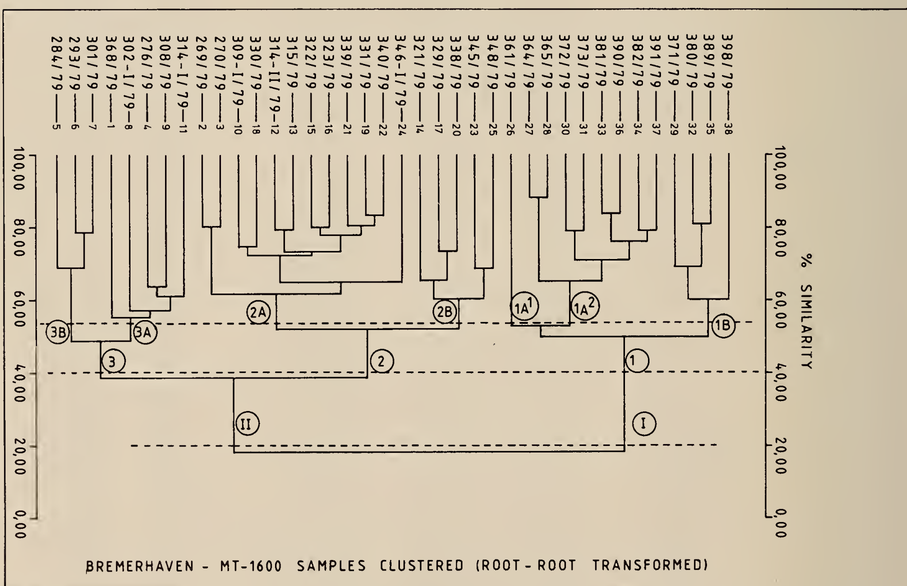


Fig. 3. Dendrogram for station affinities for MT–1600 hauls.

Group 1: which subsequently divides into three sub-groups at the 54 per cent similarity level (arbitrary choice), designated Groups 1A[1], 1A[2] and 1B (Fig. 3).

Groups 2 and 3: which are more closely related to each other than to Group 1, and which both divide into two sub-groups, also at the 54 per cent similarity level, designated Groups 2A and 2B and Groups 3A and 3B, respectively.

The ordination of the similarity matrix using MDS (Fig. 4) gives the same groupings as the dendrogram (Fig. 3). Attention should be directed to the proximity of the two stations numbered 8 (in Group 3A) and 26 (in Group 1A[1]),

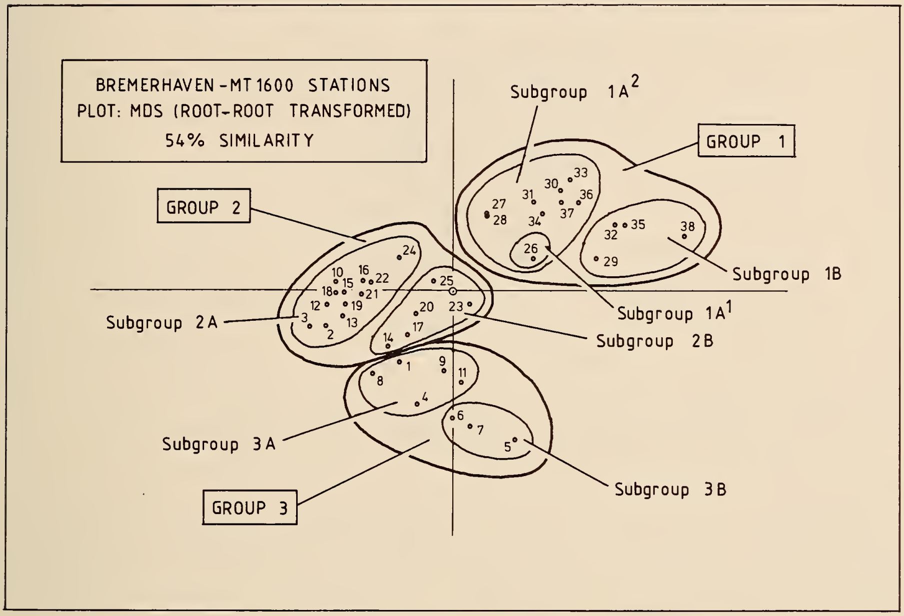


Fig. 4. MDS ordination of MT–1600 station affinities.

to Groups 2A and 1B respectively. In order to check that the dendrogram is not an artifact of the standardization employed in the manipulation of the raw data matrix, the scaling factors have been superimposed on the MDS ordination (Fig. 5). There appears to be no marked correlation, as is evident from the numerous anomalies. The correlation appears to be somewhat better if daylight and night data are superimposed on the ordination (Fig. 6). However, since the sampling programme on board was such that the deep stations were usually fished during the day and shallower stations usually at night, depth data have been superimposed on the ordination (Fig. 7) and result in the best correlation:

1. All Group 1A[2] stations are shallow hauls; all Group 1B stations are deep hauls; and the single station in Group 1A[1] (Station 26), a deep haul, has a close affinity to the deep-haul stations of Group 1B.

2. Group 2A stations are all shallow hauls, while Group 2B stations are all deep hauls.

3. Of the stations in Group 3, Station 8 (shallow haul) has a close affinity with the shallow-haul stations of Group 2A.

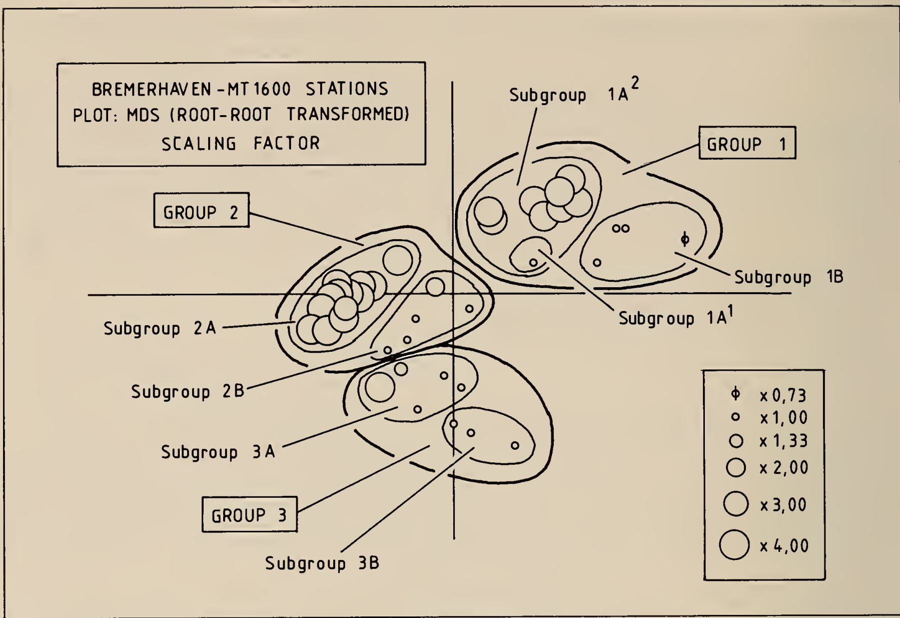


Fig. 5. Scaling factors superimposed on MDS ordination for MT-1600 hauls.

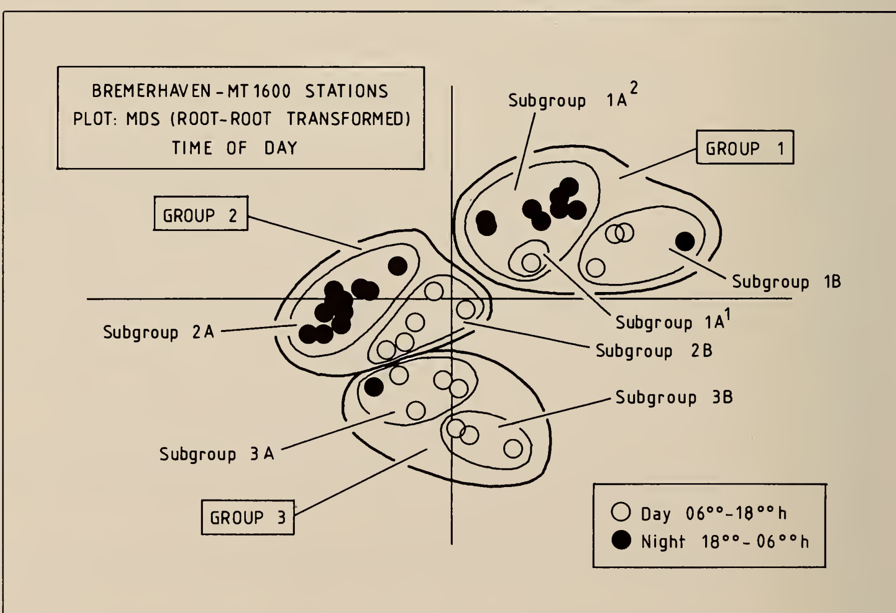


Fig. 6. Day and night data superimposed on MDS ordination for MT-1600 hauls.

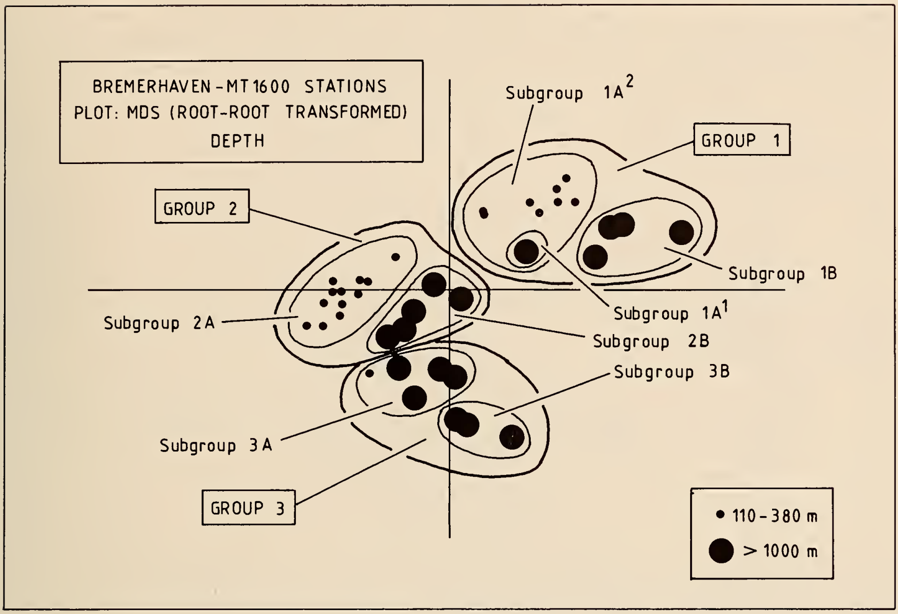


Fig. 7. Depth data superimposed on MDS ordination for MT–1600 hauls.

Geographic plots of these station groupings in terms of the Backus *et al.* (1977) regional system (Fig. 8) reveal that:

(i) Group 1 stations are all found to the north of the proposed boundary between the Temperate Region and the Subtropical Region, i.e. the 15 °C isotherm at 200 m. They are Temperate Region stations, and both deep- and shallow-haul stations belong to this group.

(ii) Group 2 stations are, in the main, found in the North Sargasso Sea Province and the North North African Subtropical Sea Province. They are Subtropical Region stations and are closely associated with Group 3 stations.

(iii) Group 3 stations are in the main in the South Sargasso Sea Province, with Group 3B representing the most southerly stations of the transect.

Of interest is the fact that at three geographical positions, both Group 2 and Group 3 elements are present. The analysis shows that in each case the shallow-haul stations are related to Group 2, i.e. they are subtropical, while the deeper-haul stations are related to Group 3. This will be discussed below.

A similar procedure was followed for the IKMT data, but was less complicated due to the fact that all hauls were at night and to about 200 m. The relationship between the computer-generated station numbers and the R.V. *Anton Dohrn* IKMT station numbers is given in Table 2. Figure 9 is the dendrogram of the station affinities, based on root-root transformed abundances of 33 species of Myctophidae taken at 14 stations. The broken line drawn at the arbitrary similarity levels of both 20 per cent and 40 per cent delimits two major

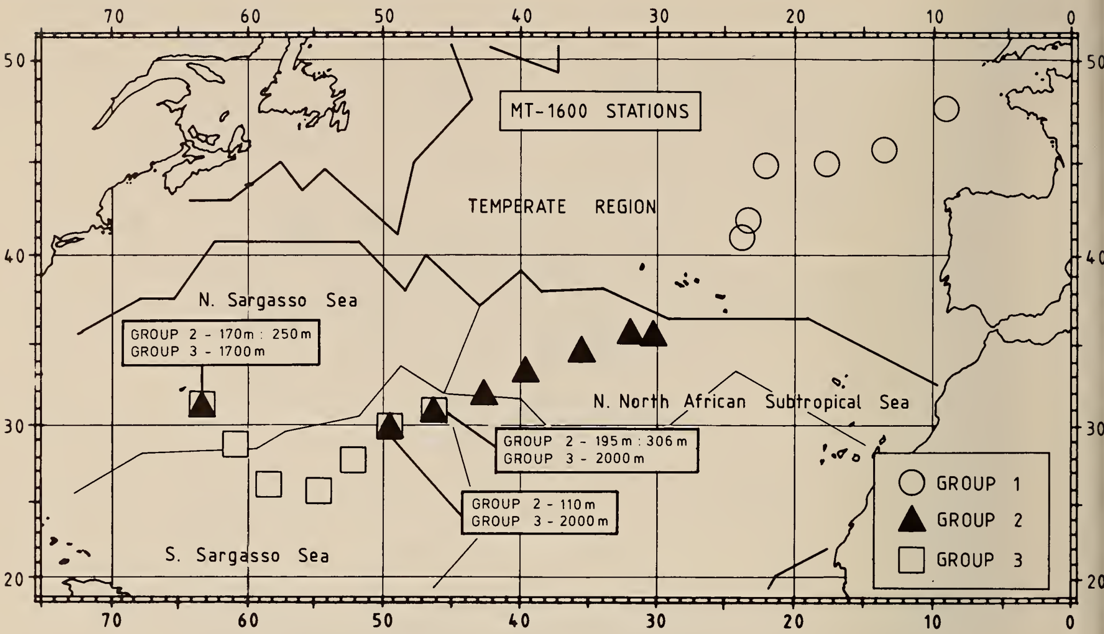


Fig. 8. Geographic plots of MT–1600 hauls showing distribution of Groups 1, 2, and 3.

TABLE 2

1979–Sargasso Sea Expedition (2nd leg). Station list of IKMT hauls indicating computer-generated station numbers and their equivalent R.V. *Anton Dohrn* station numbers.

| *Computer station no.* | *AD station no.* | *Position* | | *Date* |
|---|---|---|---|---|
| 1 | 277/79 | 28°20′N | 60°33′W | 20.04.79 |
| 2 | 286/79 | 25°52′N | 58°12′W | 21.04.79 |
| 3 | 294/79 | 25°49′N | 54°31′W | 22.04.79 |
| 4 | 302-II/79 | 27°51′N | 52°11′W | 23.04.79 |
| 5 | 309-II/79 | 29°41′N | 49°27′W | 24.04.79 |
| 6 | 316/79 | 30°48′N | 46°02′W | 25.04.79 |
| 7 | 324/79 | 31°56′N | 42°43′W | 26.04.79 |
| 8 | 332/79 | 33°04′N | 29°34′W | 27.04.79 |
| 9 | 346-II/79 | 35°23′N | 31°51′W | 29.04.79 |
| 10 | 366/79 | 42°07′N | 23°29′W | 02.05.79 |
| 11 | 374/79 | 44°56′N | 21°55′W | 03.05.79 |
| 12 | 383/79 | 44°56′N | 17°17′W | 04.05.79 |
| 13 | 399/79 | 47°44′N | 08°58′W | 06.05.79 |
| 14 | 401/79 | 47°58′N | 08°16′W | 07.05.79 |

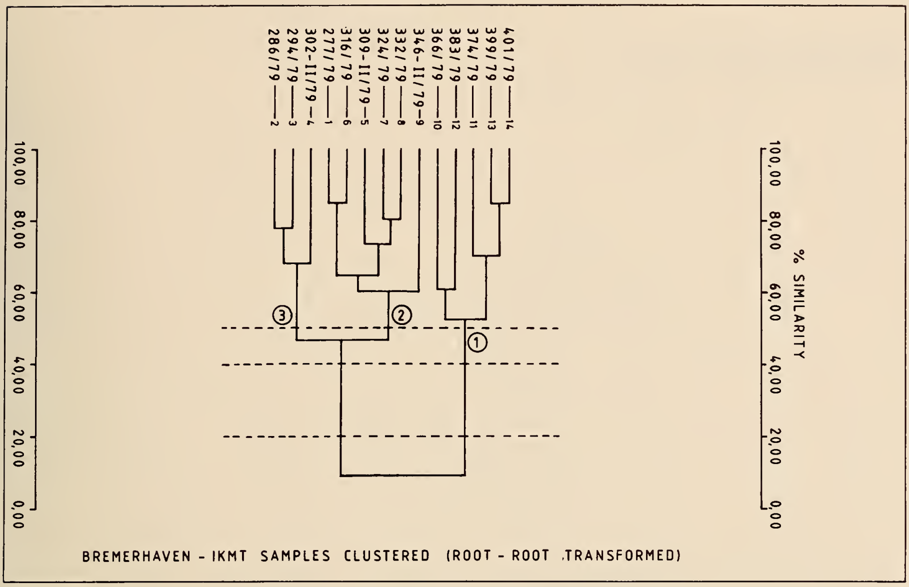


Fig. 9. Dendrogram for station affinities for IKMT hauls.

groups of stations, while the broken line drawn at the arbitrary similarity level of 50 per cent delimits three groups of stations, designated Groups 1, 2 and 3. The MDS ordination plots for the IKMT stations (Fig. 10) support this and demonstrate further that Groups 2 and 3 have a closer affinity to each other than either to Group 1. The geographical plots of the IKMT groupings (Fig. 11) support not only the results obtained from the analysis of the MT–1600 samples, but also support the ideas regarding the affinities of those stations immediately adjacent to the boundaries between the provinces of the Subtropical Region. That is, these shallow hauls show an affinity with the North Sargasso Sea or North North African Subtropical Sea Provinces within the boundaries proposed by Backus *et al.* (1977), while Group 3 stations are well within the South Sargasso Sea Province.

Examination of the temperature section for the transect (Fig. 12) reveals that there are three main hydrographic features:

1. Stations AD 275/79 through AD 305/79 are characterized by the presence of water warmer than 20 °C in the upper 50 m; by a layer of '18 °C water' between 200 m and about 400 m, the intermediate layer of the whole Sargasso Sea Region (Wegner 1979); and by the position of the 15 °C isotherm below about 500 m. These stations cover the region of the warm South Sargasso Sea Water. While Wegner (1982) points out that the convergence area is demarcated by the 21 °C and 22 °C isotherms in depths of 100 m, this feature is not well defined over the MT–1600 transect (Fig. 12; Wegner 1982, fig. 3a), due to the fact that there is a masking layer of transition water to the north. A similar condition appears to be

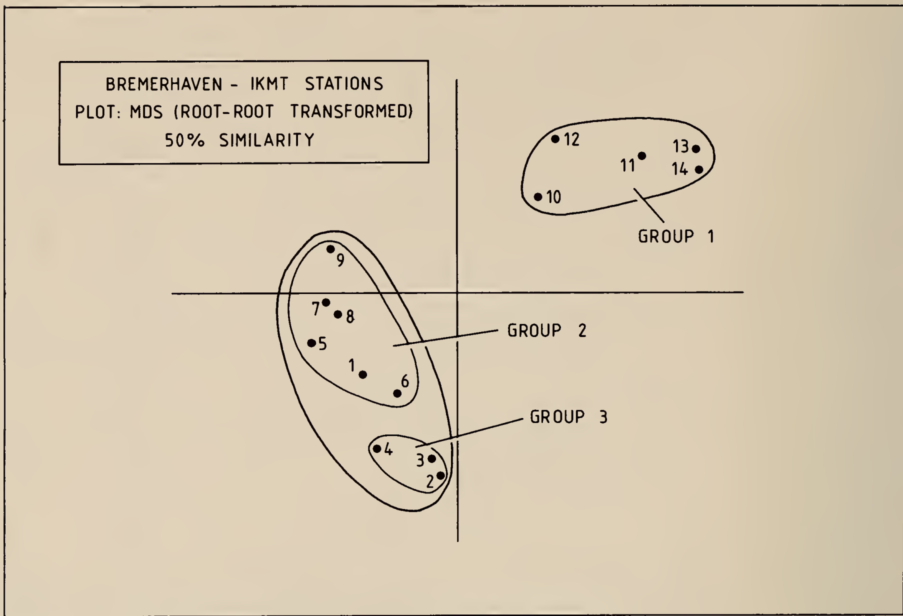


Fig. 10. MDS ordination of IKMT station affinities.

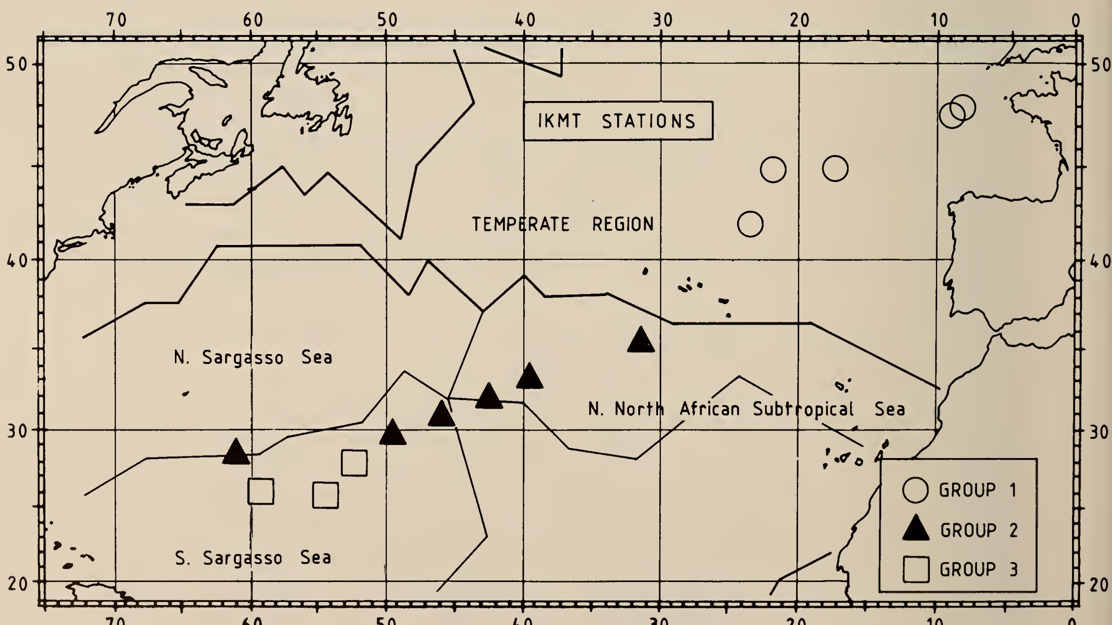


Fig. 11. Geographic plots of IKMT hauls showing distribution of Groups 1, 2, and 3.

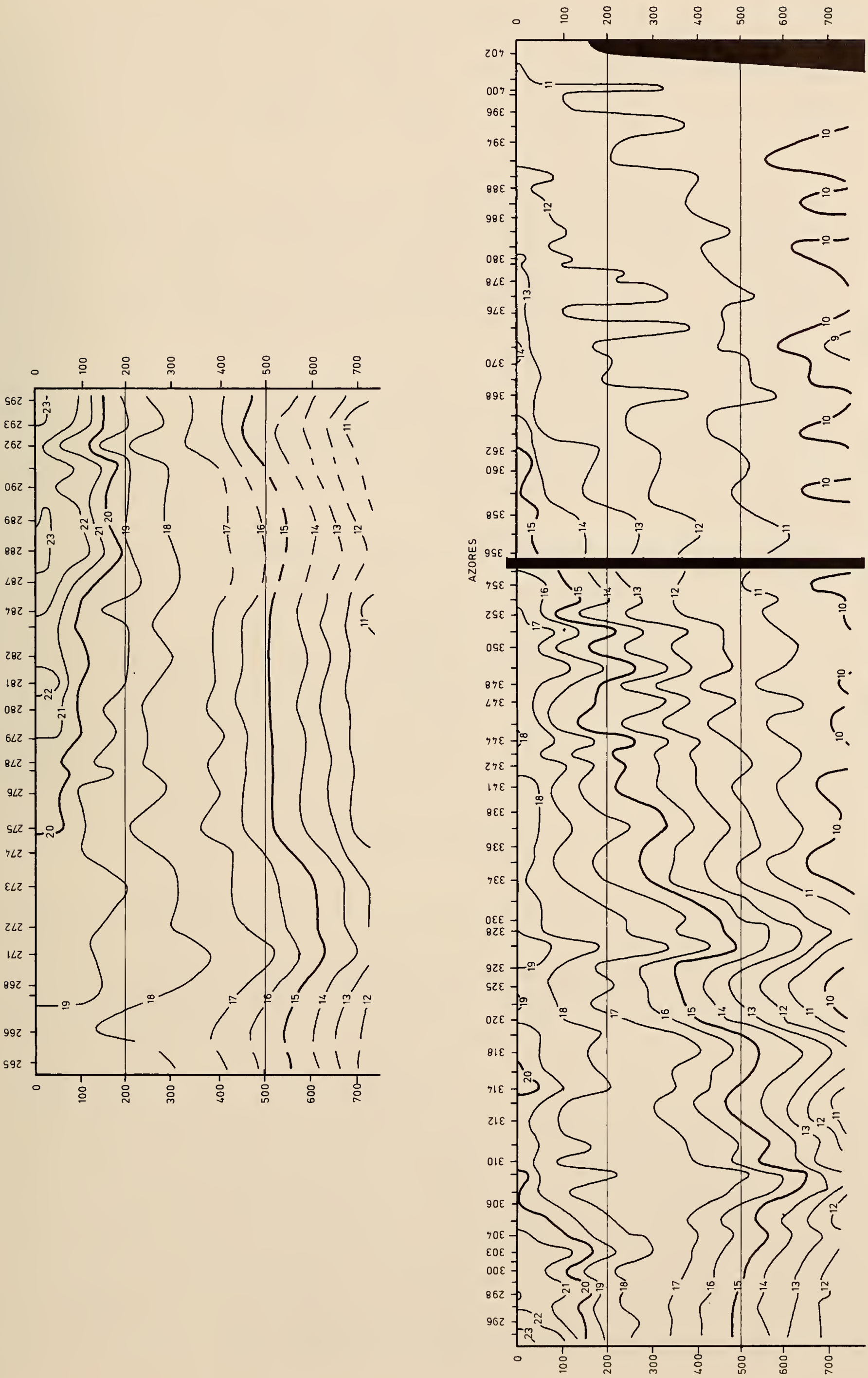


Fig. 12. Temperature section of the second leg of the 1979–Sargasso Sea Expedition (after Wegner 1979).

evident over that region which includes stations AD 306/79 through AD 318/79. Unfortunately, salinity distribution, which usually gives a better resolution for convergence determination, gave only the surface distribution across this transect (Wegner 1982). South Sargasso Sea Water probably occurred from about AD 279/79 to AD 306/79. On the basis of the biological analysis, the stations from this region represent those of Group 3.

2. Stations AD 321/79 through AD 351/79 are characterized by water of 17–19 °C, which replaces the warm South Sargasso Sea Water (>20 °C) in the upper 150 m; the absence of '18 °C water' in depths of 200 m to 400 m; the position of the 15 °C isotherm between 200 m and 500 m; and the position of the 11 °C isotherm in depths below 500 m (550–650 m). Group 2 stations are found over this region of the transect.

3. Stations AD 352/79 through AD 403/79, which include the biological sampling stations AD 361/79 to AD 401/79, are characterized by the position of the 15 °C isotherm in depths shallower than 200 m; and by the position of the 11 °C isotherm in depths shallower than about 500 m. The biological grouping of these stations is Group 1.

A summary of these relationships is given in Table 3.

TABLE 3

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Relationships of the myctophid MDS-ordination analysis to temperatures at depth.

| *Depth* (m) | *Temperatures* (°C) | | |
|---|---|---|---|
| | *Group 1* | *Group 2* | *Group 3* |
| 100 | <15 | 15–19 | >20 |
| 500 | <11 | 12–15 | >15 |

As has been pointed out above, at certain geographic positions (AD 268/79–270/79; AD 308/79–309-I/79; AD 314-I/79–315/79) both Group 2 stations (hauls to 250 m) and Group 3 stations (hauls below 1 700 m) were present. As can be seen in Figure 12, the temperature profiles at these positions reveal that, while the 15 °C isotherm lies below 500 m and there is '18 °C water' between 200 m and 400 m, conditions that approximate those for Group 3 stations, the temperature regime in the upper 200 m is characteristic of Group 2 stations, i.e. those of the North Sargasso Sea and North North African Subtropical Provinces and the transition zones immediately adjacent to the convergence. The inclusion of the MT–1600 station, AD 276/79 (*c.* 1 800 m), of Group 3, with the adjacent IKMT–station, AD 277/79 (100 f.w.o.) of Group 2, would tend to support the temperature parameters suggested above, particularly if the position of the convergence is defined according to Wegner's (1982) criteria.

The groupings for the shallow-haul stations from both the MT–1600 and the IKMT transects have been amalgamated and isohalines at 200 m, taken from Wüst & Defant (1936), have been superimposed on a geographical plot (Fig. 13), in order to elucidate relationships of these groups to salinity. The relationship of the Group 3 stations to the region of high salinity is fairly good. Since the lens of

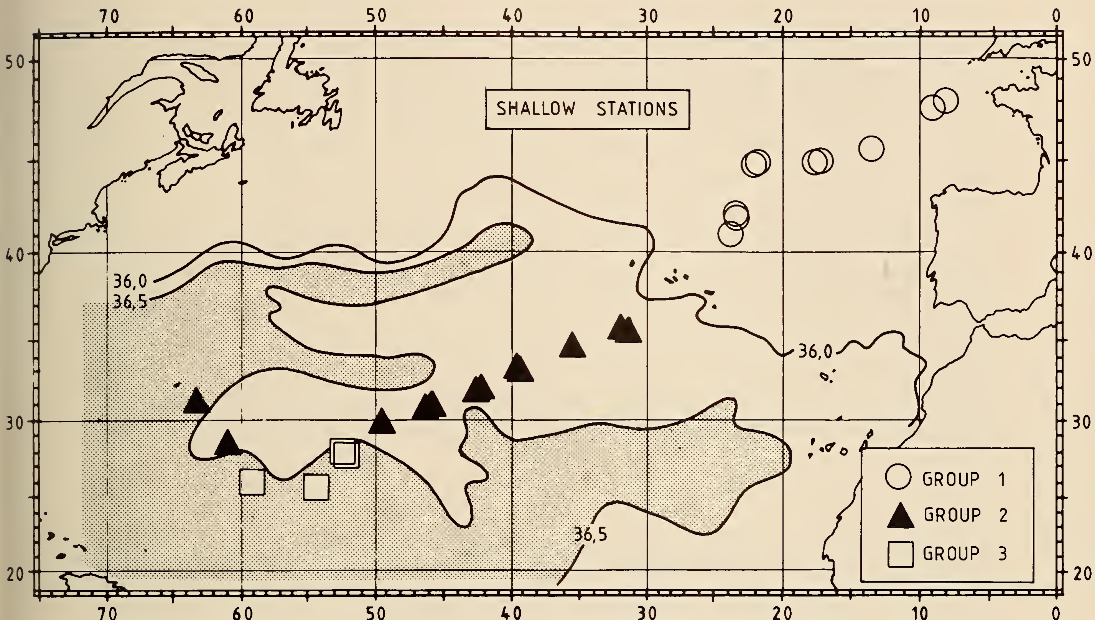


Fig. 13. Geographic plots of shallow stations (MT–1600 and IKMT) in relation to isohalines, from Wüst & Defant (1936).

high-temperature and high-salinity water at the gyral-eye is inclined from 200 m in the west to 800–1 000 m in the east, and since this warm, saline water extends farther to the east and north-east at greater depths than at shallower depths (as indicated by isohaline examination in Wüst & Defant 1936), the above interpretation of these data may be correct.

*Indicator species and community structure*

In discussing these topics with regard to the 1979–transect, several facts should be borne in mind. Firstly, $2\Delta I_i$ has approximate chi-square distribution but lacks statistical rigour (Field *et al.* 1982). The scores of $2\Delta I_i > 3{,}84$ (5% probability level) and $2\Delta I_i > 6{,}63$ (1% probability level) are therefore only employed as a 'rule of thumb' for the cut-off limits. Secondly, it is evident to us that certain small species (*Diogenichthys atlanticus* and *Notolychnus valdiviae*) and surface migrators (*Gonichthys cocco, Myctophum nitidulum*, and *Symbolophorus rufinus*) are not well represented in MT–1600 samples. This may be due to the mesh size in front of the cod-end liner of the MT–1600, or the fact that on hauling the MT–1600 collapses just below the surface, or both. Other species (*Lampadena anomala, Loweina interrupta*, and *Loweina rara*) may indeed be uncommon. Thirdly, our data result from a single transect. Therefore seasonal changes in distributional range and seasonal variability in myctophid community structure cannot be discussed. Unpublished data from more recent cruises have indicated that this may be of importance, e.g. in *Bolinichthys supralateralis, Diaphus dumerilii*, and *Lampadena urophaos atlantica*. Finally, and in addition to its known inefficiency in sampling the myctophid fauna, the IKMT was fished only to 200 m, thereby biasing the results for the deeper-living species (*Lampanyctus crocodilus* and *L. photonotus*). Only about half (52,38 %) of the species caught by the MT–1600 are represented in the IKMT samples. Therefore a table of the indicator species only is presented for the IKMT data (Table 8).

Results of information statistic ($I$-) tests for the MT–1600 data, which are calculated from the numbers of specimens (density), are presented in Tables 4, 5 and 6. Table 4 lists the species that are characteristic of Group 1 and distinguish them from combined species of Group 2 and Group 3. There are no 'perfect' indicator species. That is, there are no species that occur in all samples of Group 1 and in none of the samples of the compared groups. However, all those species listed may be considered to be indicators, whose presence or absence at stations

TABLE 4

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence ($F$) and numbers of individuals ($N$) of species, ranked according to information statistics, which distinguish Group 1 ($F_1$, $N_1$) from Groups 2 and 3 ($F_{2+3}$, $N_{2+3}$). $2\Delta I_i$ values are calculated from numbers of specimens. Species above horizontal dotted line have $2\Delta I_i > 6,63$; those below line have $2\Delta I_i > 3,84$; species with $2\Delta I_i < 3,84$ are not included. Maximum values for $F_1$ and $F_{2+3}$ are given in parentheses.

| Species | $F_1$ (13) | $N_1$ | $F_{2+3}$ (25) | $N_{2+3}$ | $2\Delta I$ |
|---|---|---|---|---|---|
| *Benthosema glaciale* | 13 | 11 698 | 1 | 4 | 25 026,911 |
| *Notoscopelus kroeyerii* | 12 | 7 163 | 0 | 0 | 15 366,595 |
| *Myctophum punctatum* | 12 | 1 969 | 1 | 4 | 4 169,793 |
| *Ceratoscopelus maderensis* | 10 | 613 | 3 | 70 | 922,185 |
| *Symbolophorus veranyi* | 11 | 494 | 6 | 32 | 845,378 |
| *Notoscopelus bolini* | 5 | 743 | 8 | 187 | 817,022 |
| *Electrona risso* | 12 | 437 | 3 | 21 | 784,590 |
| *Diaphus holti* | 11 | 394 | 2 | 46 | 588,997 |
| *Lampanyctus crocodilus* | 13 | 285 | 4 | 10 | 532,432 |
| *Diaphus rafinesquii* | 12 | 458 | 14 | 380 | 146,311 |
| *Lampanyctus intricarius* | 10 | 55 | 0 | 0 | 117,990 |
| *Lampanyctus macdonaldi* | 3 | 14 | 0 | 0 | 30,034 |
| *Lampadena speculigera* | 5 | 11 | 0 | 0 | 23,598 |
| *Protomyctophum arcticum* | 4 | 11 | 0 | 0 | 23,598 |
| *Loweina interrupta* | 1 | 4 | 0 | 0 | 8,581 |
| ........ | | | | | |
| *Diaphus metopoclampus* | 4 | 14 | 4 | 10 | 5,807 |

within the group is a function of their geographic range and/or vertical distribution pattern, e.g. *Lampanyctus macdonaldi* and *Protomyctophum arcticum*. Comparison of the frequencies of occurrence within ($F_1$) and outside ($F_{2+3}$) the group is an expression of fidelity; that is, the degree of exclusiveness that the species shows towards Group 1 (Temperate Region community), while numbers

TABLE 5

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence ($F$) and numbers of individuals ($N$) of species, ranked according to information statistics, which distinguish Group 2 ($F_2$, $N_2$) from Groups 1 and 3 ($F_{1+3}$, $N_{1+3}$). Other conventions as in Table 4.

| Species | $F_2$ (17) | $N_2$ | $F_{1+3}$ (21) | $N_{1+3}$ | $2\Delta I$ |
|---|---|---|---|---|---|
| *Ceratoscopelus warmingii* | 17 | 4 944 | 8 | 155 | 6 826,668 |
| *Hygophum hygomii* | 17 | 4 214 | 10 | 134 | 5 741,827 |
| *Lobianchia gemellarii* | 17 | 4 287 | 19 | 428 | 4 534,569 |
| *Hygophum benoiti* | 16 | 2 708 | 5 | 368 | 2 540,122 |
| *Lobianchia dofleini* | 16 | 2 166 | 5 | 198 | 2 358,445 |
| *Diaphus mollis* | 15 | 1 327 | 7 | 57 | 1 727,171 |
| *Bolinichthys indicus* | 17 | 1 474 | 12 | 292 | 1 133,791 |
| *Notoscopelus resplendens* | 17 | 625 | 1 | 13 | 893,924 |
| *Lampanyctus photonotus* | 16 | 790 | 11 | 90 | 796,776 |
| *Lampandena urophaos atlantica* | 11 | 371 | 4 | 6 | 542,372 |
| *Lepidophanes gaussi* | 14 | 447 | 4 | 37 | 501,633 |
| *Notoscopelus caudispinosus* | 16 | 331 | 5 | 18 | 412,061 |
| *Benthosema suborbitale* | 10 | 222 | 0 | 0 | 357,142 |
| *Lampadena chavesi* | 11 | 208 | 0 | 0 | 334,619 |
| *Lampanyctus festivus* | 14 | 178 | 2 | 6 | 240,593 |
| *Hygophum reinhardtii* | 15 | 208 | 4 | 16 | 238,318 |
| *Diaphus effulgens* | 8 | 142 | 2 | 5 | 190,735 |
| *Taaningichthys minimus* | 12 | 153 | 5 | 12 | 174,361 |
| *Diogenichthys atlanticus* | 12 | 101 | 1 | 1 | 152,429 |
| *Lampanyctus pusillus* | 17 | 863 | 14 | 566 | 140,861 |
| *Lampanyctus ater* | 13 | 227 | 9 | 62 | 138,223 |
| *Lepidophanes guentheri* | 8 | 142 | 4 | 21 | 128,113 |
| *Diaphus lucidus* | 8 | 64 | 0 | 0 | 102,960 |
| *Diaphus splendidus* | 6 | 60 | 0 | 0 | 96,525 |
| *Diaphus brachycephalus* | 7 | 72 | 1 | 3 | 94,196 |
| *Loweina rara* | 6 | 37 | 0 | 0 | 59,524 |
| *Diaphus problematicus* | 3 | 32 | 0 | 0 | 51,480 |
| *Diaphus perspicillatus* | 3 | 31 | 1 | 1 | 42,157 |
| *Notolychnus valdiviae* | 3 | 26 | 0 | 0 | 41,827 |
| *Myctophum selenops* | 7 | 45 | 2 | 9 | 34,408 |
| *Diaphus dumerilii* | 4 | 21 | 0 | 0 | 33,784 |
| *Hygophum taaningi* | 2 | 48 | 4 | 14 | 27,590 |
| *Bolinichthys photothorax* | 2 | 11 | 0 | 0 | 17,696 |
| *Centrobranchus nigroocellatus* | 2 | 5 | 0 | 0 | 8,004 |
| *Diaphus bertelseni* | 2 | 5 | 0 | 0 | 8,004 |
| *Lampanyctus lineatus* | 7 | 26 | 5 | 14 | 6,637 |
| ............ | | | | | |
| *Diaphus termophilus* | 1 | 4 | 0 | 0 | 6,435 |
| *Lampanyctus nobilis* | 1 | 4 | 0 | 0 | 6,435 |
| *Lampanyctus alatus* | 1 | 4 | 0 | 0 | 6,435 |

TABLE 6

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence ($F$) and numbers of individuals ($N$) of species, ranked according to information statistics, which distinguish Group 3 ($F_3$, $N_3$) from Groups 1 and 2 ($F_{1+2}$, $N_{1+2}$). Other conventions as in Table 4.

| Species | $F_3$ (8) | $N_3$ | $F_{1+2}$ (30) | $N_{1+2}$ | $2\Delta I$ |
|---|---|---|---|---|---|
| *Lampanyctus cuprarius* | 8 | 184 | 13 | 126 | 214,132 |

of individuals ($N_1$) are indicative of their relative abundance. A plot of cumulative percentage densities for those ranked species with $2\Delta I_i > 6{,}63$ (Fig. 14) reveals that 5 species (*Benthosema glaciale, Notoscopelus kroeyerii, Myctophum punctatum, Notoscopelus bolini*, and *Ceratoscopelus maderensis*) are dominant and comprise about 90 per cent of the total. The $N_1$ and $N_{2+3}$ values for *Notoscopelus bolini* are high, and the sampled material consists mainly of very small juvenile specimens (SL 24–42 mm). Only a single adult specimen (SL 92 mm) of this species was taken during the transect (in the Group 1 area). A similar bias is evident in the IKMT samples (see below). Shannon diversity indices ($H$) for the Group 1 stations (MT–1600 samples) were calculated using:

$$H = \frac{n \log_{10} n - \sum_{i=1}^{k} f_i \log_{10} f_i}{n}$$

$H$ values ranged between 0,42 and 1,12 (Table 7). Of the 15 species (with $2\Delta I_i > 6{,}63$) involved in this community, 10 are endemic to the temperate North Atlantic, 4 possess a Bitemperate Pattern and 1 species, *Electrona risso*, is said to have either an Eastern Pattern (Backus *et al.* 1977) or a Widespread Pattern (Hulley 1981). Two genera are represented by 2 species each (*Diaphus holti, D. rafinesquii, Notoscopelus bolini*, and *N. kroeyerii*) and one genus by 3 species (*Lampanyctus crocodilus, L. intricarius*, and *L. macdonaldi*). In relation to niche separation, data from the 1982–Mid-Atlantic Ridge and 1983–TIFI–8 cruises indicate possible differences in spawning season and a noticeable degree of vertical separation of adult specimens of the *Lampanyctus* species, while *Notoscopelus kroeyerii* may well have to be re-assessed as a pseudoceanic species (unpublished data). Comment on the association of *Diaphus holti* with Mediterranean Outflow Water has already been made (Hulley 1981).

Similarly, Table 5 lists those species that are characteristic of Group 2 and distinguish it from Groups 1 and 3. Again, there are no 'perfect' indicator species for the group, but *Notoscopelus resplendens* is always present in Group 2 and occurs very rarely (only once, with 13 specimens) in the other groups. There are only 5 species that are endemic to the Atlantic; 19 species have Broadly Tropical Patterns, 11 have Subtropical Patterns, 5 have Tropical Patterns, 3 have

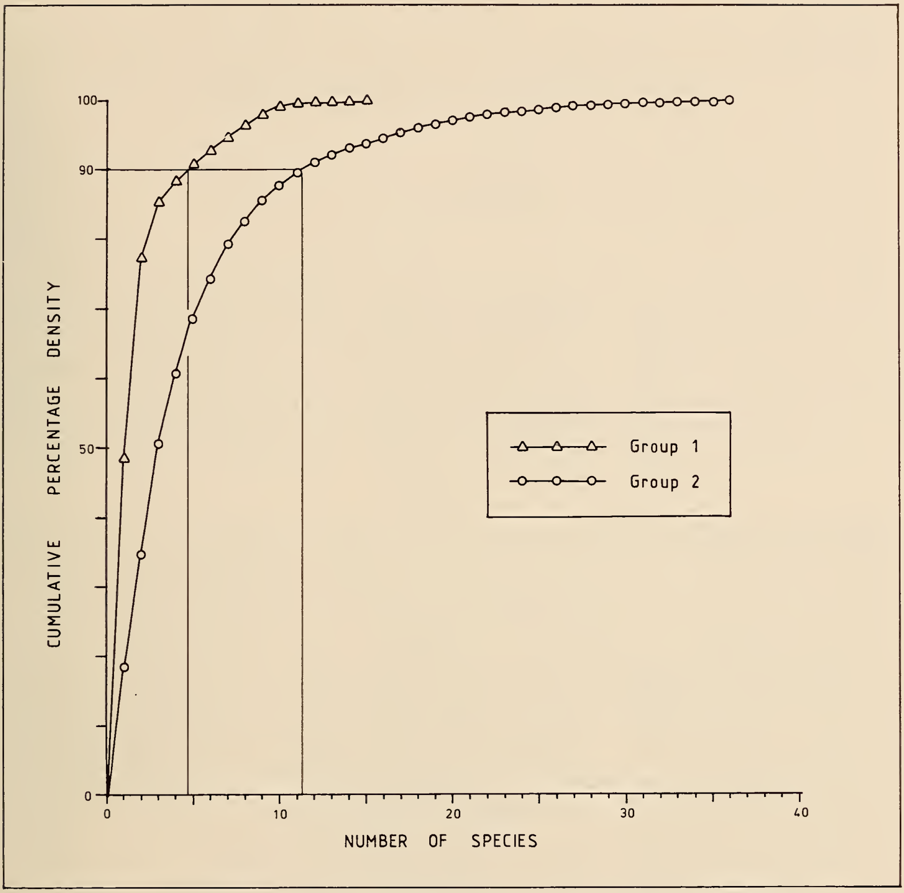


Fig. 14. Graph of cumulative percentage densities for Group 1 and Group 2.

Widespread Patterns, and 1 species (*Hygophum benoiti*) is said to have a North Temperate Pattern (Hulley 1981). Cumulative percentage density plots (Fig. 14) reveal that 11 species (with $2\triangle I_i > 6{,}63$) comprise about 90 per cent of the total, more than double the number in Group 1. Shannon diversity indices ($H$) for the stations range between 0,91 and 1,21 (Table 7). It should be noted that *Hygophum benoiti*, which has been included in the Temperate-subtropical Subpattern of the Cool Water Group (Hulley 1981), is a Group 2 indicator.

Only one species (*Lampanyctus cuprarius*, an Atlantic endemic) is characteristic of Group 3, when compared with Groups 1 and 2 (Table 6). It would appear therefore that the community structure of Group 3 is not different from that of Group 2 and that the distinction of these two groups is based rather on species abundances. This feature has already been noted (Backus *et al.* 1969) and is probably linked to differences in food supply, as indicated by the primary

Table 7

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Shannon Index of Diversity (*H*) and Evenness (*J*) based on 63 myctophid species. Maximum depth of haul in metres; computer station number in parenthesis, following AD station numbers.

| Depths: 0–210 m | Depths: 211–350 m | Depths: >1 800 m | Latitude |
|---|---|---|---|
| **Group 1** ($H_{max}$ = 1,79) | | | |
| | | 398/79 (38) *H* = 0,52 *J* = 0,29 | 48°N |
| 390/79 (36) *H* = 0,47 *J* = 0,26 | 391/79 (37) *H* = 0,60 *J* = 0,33 | 389/79 (35) *H* = 0,81 *J* = 0,45 | 46°N |
| 381/79 (33) *H* = 0,47 *J* = 0,26 | 382/79 (34) *H* = 0,64 *J* = 0,35 | 380/79 (32) *H* = 0,85 *J* = 0,47 | 45°N |
| 372/79 (30) *H* = 0,54 *J* = 0,30 | 373/79 (31) *H* = 0,42 *J* = 0,24 | 371/79 (29) *H* = 0,61 *J* = 0,34 | 45°N |
| 364/79 (27) *H* = 0,95 *J* = 0,53 | 365/79 (28) *H* = 0,77 *J* = 0,43 | 361/79 (26) *H* = 1,12 *J* = 0,62 | 42°N |
| **Group 2** ($H_{max}$ = 1,79) | | | |
| | | 348/79 (25) *H* = 1,16 *J* = 0,64 | 35°N |
| | 346/79 (24) *H* = 0,94 *J* = 0,53 | 345/79 (23) *H* = 1,14 *J* = 0,64 | 35°N |
| 339/79 (21) *H* = 1,09 *J* = 0,61 | 340/79 (22) *H* = 1,17 *J* = 0,65 | 338/79 (20) *H* = 1,07 *J* = 0,60 | 34°N |
| 330/79 (18) *H* = 1,01 *J* = 0,56 | 331/79 (19) *H* = 1,21 *J* = 0,67 | 329/79 (17) *H* = 1,08 *J* = 0,60 | 33°N |
| 322/79 (15) *H* = 0,94 *J* = 0,52 | 323/79 (16) *H* = 1,07 *J* = 0,59 | 321/79 (14) *H* = 1,12 *J* = 0,62 | 32°N |
| 314/79 (12) *H* = 0,97 *J* = 0,54 | 315/79 (13) *H* = 1,05 *J* = 0,58 | | 31°N |
| 269/79 (2) *H* = 0,91 *J* = 0,51 | 270/79 (3) *H* = 0,93 *J* = 0,52 | | 31°N |
| 309/79 (10) *H* = 0,91 *J* = 0,51 | | | 30°N |
| **Group 3** ($H_{max}$ = 1,79) | | | |
| | | 268/79 (1) *H* = 1,07 *J* = 0,60 | 31°N |
| | | 314/79 (11) *H* = 0,86 *J* = 0,48 | 31°N |
| | | 308/79 (9) *H* = 0,76 *J* = 0,42 | 30°N |
| | | 276/79 (4) *H* = 0,94 *J* = 0,52 | 29°N |
| | 302/79 (8) *H* = 0,97 *J* = 0,54 | 301/79 (7) *H* = 0,98 *J* = 0,55 | 28°N |
| | | 293/79 (6) *H* = 1,00 *J* = 0,56 | 26°N |
| | | 284/79 (5) *H* = 0,80 *J* = 0,45 | 26°N |

productivity values of the two areas (Hela & Laevastu 1962). However, examination of our data and those of Nafpaktitis *et al.* (1977) reveals that the following species, present in Group 2, have never been recorded from the South Sargasso Sea Province: *Diaphus bertelseni, D. lucidus, Lampadena chavesi,* and *Notoscopelus bolini. Hygophum hygomii* occurs at seven of the eight MT–1600 stations of Group 3 and is represented in the IKMT data by a single specimen (SL 17 mm) from 27°51′N 52°11′W. Shannon diversity indices for Group 3 stations range between 0,76 and 1,07 (Table 7).

Table 8 lists the indicator species extracted from the IKMT data using information statistics. In general, there is good agreement between this set and the set obtained from our MT–1600 data (Tables 4–6). However, there are three exceptions (*Lampanyctus crocodilus, L. photonotus*, and *Notoscopelus bolini*). These, we feel, are a reflection of the limitations of the IKMT sampling method (see above) and should therefore be treated with extreme caution.

TABLE 8

1979–Sargasso Sea Expedition (2nd leg). IKMT hauls: Indicator species based on information statistic (*I*-) tests, where $2\Delta I_i > 6{,}63$. Anomalous species (marked with an asterisk) are discussed in the text.

| Group 1 | Group 2 | Group 3 |
|---|---|---|
| *Benthosema glaciale* | *Benthosema suborbitale* | **Lampanyctus photonotus* |
| *Ceratoscopelus maderensis* | *Bolinichthys indicus* | |
| *Myctophum punctatum* | *Ceratoscopelus warmingii* | |
| *Notoscopelus kroeyerii* | *Diogenichthys atlanticus* | |
| | *Hygophum hygomii* | |
| | **Lampanyctus crocodilus* | |
| | *Lampanyctus pusillus* | |
| | *Lepidophanes gaussi* | |
| | *Lobianchia dofleini* | |
| | *Lobianchia gemellarii* | |
| | **Notoscopelus bolini* | |
| | *Notoscopelus resplendens* | |

In summary then, the number of species comprising the myctophid community in Group 1 (North Atlantic Temperate Region) is less than the number in Groups 2 and 3 (North Atlantic Subtropical Region), with correspon- ding lower values for the index of diversity, but a greater degree of dominance among the most abundant species. The apparent increase in the species diversity index (*H*) with increasing depth (Table 7) is an artifact. The MT–1600, which is not an opening and closing net, samples the entire water column to the maximum fishing depth of a particular haul.

Because of this, detailed examination of the correlation between fishing depth and the subgroupings within each of Groups 1, 2, and 3 is somewhat presumptuous. Such discussion is further constrained by the variable nature of the sampling programme carried out during the transect. Firstly, two shallow hauls and their associated deep haul were not made at each sampling position; except at a single station (AD 302-I/79), all Group 3 hauls were deep (Fig. 7); and only in the case of the Group 2 stations were shallow hauls (110–380 m) made at night and corresponding deep hauls (1 300–1 950 m) made during the day (Fig. 6). Secondly, shallow night hauls were aimed at just below or just above the deep scattering layer (DSL) read from echo-sounder traces; deep day hauls were fished either as deep as possible, the depth being determined from the depth-time recorder on completion of the haul, or to an arbitrary selected depth of about 2 000 m, dictated by the length of trawling warp deployed. However, in order to assess which species differ most between these subgroupings information statistic tests were performed on the relevant data. The results of the tests are presented in Tables 9, 10, and 11.

Table 9 lists the species that are characteristic of Groups 1A and 1B. No species occurs at all stations in one group and in none of the samples of the other group, although *Ceratoscopelus maderensis* and *Lampanyctus intricarius* approxi-

TABLE 9

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence ($F$) and numbers of individuals ($N$) of species, ranked according to information statistics, which distinguish Group 1A ($F_{1A}$, $N_{1A}$) from Group 1B ($F_{1B}$, $N_{1B}$). Asterisks (*) refer to Group 2 indicator species. Other conventions as in Table 4.

| Species | $F_{1A}$ (9) | $N_{1A}$ | $F_{1B}$ (4) | $N_{1B}$ | $2\Delta I$ |
|---|---|---|---|---|---|
| **Group 1A** | | | | | |
| *Benthosema glaciale* | 9 | 11 439 | 4 | 259 | 6 537,369 |
| *Notoscopelus kroeyerii* | 9 | 7 062 | 3 | 101 | 4 370,428 |
| *Myctophum punctatum* | 8 | 1 940 | 4 | 29 | 1 192,920 |
| *Notoscopelus bolini* | 4 | 742 | 1 | 1 | 532,841 |
| *Ceratoscopelus maderensis* | 9 | 612 | 1 | 1 | 437,617 |
| **Lampanyctus pusillus* | 9 | 559 | 2 | 4 | 372,998 |
| *Symbolophorus veranyi* | 8 | 485 | 3 | 9 | 287,978 |
| **Hygophum benoiti* | 5 | 368 | 0 | 0 | 270,645 |
| *Diaphus rafinesquii* | 9 | 439 | 3 | 19 | 209,518 |
| **Bolinichthys indicus* | 4 | 255 | 1 | 1 | 176,811 |
| *Diaphus holti* | 8 | 376 | 3 | 18 | 172,701 |
| *Electrona risso* | 8 | 411 | 4 | 26 | 166,403 |
| **Lobianchia dofleini* | 3 | 192 | 0 | 0 | 141,206 |
| **Lobianchia gemellarii* | 8 | 238 | 4 | 32 | 53,931 |
| **Hygophum hygomii* | 3 | 66 | 0 | 0 | 48,540 |
| **Lampanyctus ater* | 5 | 58 | 1 | 2 | 29,833 |
| **Lampanyctus photonotus* | 4 | 32 | 0 | 0 | 23,534 |
| *Lampanyctus intricarius* | 8 | 51 | 2 | 4 | 18,267 |
| *Lampanyctus crocodilus* | 9 | 222 | 4 | 63 | 10,685 |
| *Diaphus metopoclampus* | 4 | 14 | 0 | 0 | 10,296 |
| ........ | | | | | |
| **Gonichthys cocco* | 2 | 6 | 0 | 0 | 4,413 |
| **Group 1B** | | | | | |
| *Lampanyctus macdonaldi* | 0 | 0 | 3 | 14 | 33,002 |

mate this condition for Group 1A and *Lampanyctus macdonaldi* for Group 1B. In the main, differences in abundances are responsible for the high $2\Delta I_i$ values. Bearing in mind both the constraints pointed out above and the vertical distribution data given in the literature, it would appear either that day samples (*c.* 2 000 m) were below the depths of maximum abundance of the species and night samples (155–350 m) were targeted at depths of maximum abundance, or that the species are more dispersed vertically in the water column during the day than at night, or both. The first ten species, ranked according to their $2\Delta I_i$ values, have their maximum abundance in the upper 100 m at night. During the Mid-Atlantic Ridge cruise in June 1982, *Lampanyctus macdonaldi* was not taken at depths less than 870 m, while during the TIFI–8 cruise in May 1983, it was not taken at depths shallower than 600 m (ISH unpublished data), both of which would support the result in Table 9. Certain subtropical species (Group 2 indicators: *Bolinichthys indicus, Gonichthys cocco, Hygophum benoiti, Hygophum hygomii, Lampanyctus ater, Lampanyctus photonotus, Lampanyctus pusillus, Lobianchia dofleini*), which transgress the boundary zone into the Temperate Region, also serve to distinguish Group 1A from Group 1B. As is to be expected, they are either absent from the deeper (= colder; see Fig. 12) samples of Group 1B or occur in small numbers, perhaps representing contamination of the catch when the net is heaved through the overlying warmer water layers. The higher values for *Lobianchia gemellarii* in both Group 1A and Group 1B (Table 9) could be accounted for by the expatriate distribution pattern of this species in the temperate North Atlantic (Hulley 1981). *Gonichthys cocco*, a surface-migrating broadly tropical species, is not well sampled by the MT–1600 (p. 33), so that its inclusion in Table 9 should be treated with reservation.

Table 10 lists the species that serve to distinguish Group 2A (shallow night hauls: 110–380 m) from Group 2B (deep day hauls: 1 300–1 950 m). Again, no species occur in all samples of Group 2A and in none of Group 2B or vice versa. Higher abundance values at night are responsible for the two groupings. Only two temperate species (Group 1 indicators: *Diaphus holti, Notoscopelus bolini*) are included in Group 2A. As pointed out above, *Notoscopelus bolini* samples taken during the transect, south of the boundary between the Temperate and Subtropical Regions, are small juveniles (22–42 mm), while *Diaphus holti* was recorded only from the two stations immediately to the south of the boundary zone. Two species are characteristic of Group 2B: *Taaningichthys bathyphilus*, a bathypelagic widespread species, is known only from depths below 500 m; and *Electrona risso*, a Group 1 (Table 4) indicator species. The present analysis suggests that *Electrona risso* may occupy shallower depths in the Temperate Region than it does in the Subtropical Region.

The separation of Group 3A from Group 3B appears to be related to geographical position rather than to depth. One shallow haul only is included in Group 3 and the hauls of Group 3B represent the most southerly stations occupied during the transect. As pointed out above, differences between Group 2 and Group 3 stations rest primarily on the relative abundances of the species in

TABLE 10

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence (*F*) and numbers of individuals (*N*) of species, ranked according to information statistics, which distinguish Group 2A ($F_{2A}$, $N_{2A}$) from Group 2B ($F_{2B}$, $N_{2B}$). Asterisks (*) refer to Group 1 indicator species; dagger signs (†) refer to Group 3 indicator species. Other conventions as in Table 4.

| Species | $F_{2A}$ (12) | $N_{2A}$ | $F_{2B}$ (5) | $N_{2B}$ | $2\Delta I$ |
|---|---|---|---|---|---|
| **Group 2A** | | | | | |
| *Lobianchia gemellarii* | 12 | 4 212 | 5 | 75 | 2 362,144 |
| *Hygophum hygomii* | 12 | 4 116 | 5 | 98 | 2 176,223 |
| *Ceratoscopelus warmingii* | 12 | 4 739 | 5 | 255 | 1 911,513 |
| *Hygophum benoiti* | 11 | 2 626 | 5 | 82 | 1 294,966 |
| *Lobianchia dofleini* | 11 | 2 122 | 5 | 44 | 1 155,918 |
| *Bolinichthys indicus* | 12 | 1 432 | 5 | 42 | 718,678 |
| *Diaphus mollis* | 12 | 1 299 | 4 | 28 | 701,953 |
| *Lampanyctus photonotus* | 12 | 781 | 4 | 9 | 467,639 |
| *Lampanyctus pusillus* | 12 | 831 | 5 | 32 | 383,549 |
| *Lepidophanes gaussi* | 11 | 442 | 3 | 5 | 265,266 |
| *Lampadena urophaos atlantica* | 9 | 369 | 2 | 2 | 237,064 |
| *Notoscopelus resplendens* | 12 | 584 | 5 | 41 | 204,540 |
| *Notoscopelus caudispinosus* | 12 | 318 | 4 | 13 | 143,692 |
| *Benthosema suborbitale* | 9 | 220 | 1 | 2 | 135,220 |
| *Lampadena chavesi* | 9 | 200 | 2 | 8 | 91,085 |
| *Hygophum reinhardtii* | 11 | 198 | 4 | 10 | 82,195 |
| *Lepidophanes guentheri* | 6 | 140 | 2 | 2 | 81,399 |
| *Diaphus effulgens* | 7 | 139 | 1 | 3 | 75,092 |
| *Taaningichthys minimus* | 9 | 147 | 3 | 6 | 66,462 |
| **Notoscopelus bolini* | 5 | 176 | 3 | 11 | 65,856 |
| *Lampanyctus festivus* | 11 | 168 | 3 | 10 | 64,495 |
| *Diaphus splendidus* | 6 | 60 | 0 | 0 | 41,797 |
| *Diaphus brachycephalus* | 6 | 71 | 1 | 1 | 41,368 |
| *Hygophum taaningi* | 2 | 48 | 0 | 0 | 33,437 |
| *Diaphus lucidus* | 7 | 61 | 1 | 3 | 25,617 |
| *Diaphus problematicus* | 3 | 32 | 0 | 0 | 22,292 |
| *Diaphus perspicillatus* | 3 | 31 | 0 | 0 | 21,595 |
| **Diaphus holti* | 1 | 43 | 1 | 2 | 19,092 |
| *Myctophum selenops* | 6 | 43 | 1 | 2 | 18,486 |
| *Notolychnus valdiviae* | 3 | 26 | 0 | 0 | 18,112 |
| *Lampanyctus ater* | 8 | 186 | 5 | 41 | 15,483 |
| *Diaphus dumerilii* | 4 | 21 | 0 | 0 | 14,629 |
| †*Lampanyctus cuprarius* | 8 | 106 | 5 | 20 | 12,527 |
| **Group 2B** | | | | | |
| *Taaningichthys bathyphilus* | 0 | 0 | 3 | 10 | 24,476 |
| **Electrona risso* | 1 | 8 | 2 | 13 | 9,481 |

the two groups. This can be linked to differences in food supply, as indicated by primary productivity values for the two geographic areas. The inclusion of a single species, *Hygophum taaningi* (Broadly Tropical Pattern: Thermophilic Eurytropical Subpattern), in Group 3B (Table 11) would tend to support this hypothesis, since the species has a comparatively shallow night distribution between the surface and 250 m.

TABLE 11

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Frequencies of occurrence ($F$) and numbers of individuals ($N$) of species, ranked according to information statistics, which distinguish Group 3A ($F_{3A}$, $N_{3A}$) from Group 3B ($F_{3B}$, $N_{3B}$). Asterisks (*) refer to Group 2 indicator species. Other conventions as in Table 4.

| Species | $F_{3A}$ (5) | $N_{3A}$ | $F_{3B}$ (3) | $N_{3B}$ | $2\Delta I$ |
|---|---|---|---|---|---|
| **Group 3A** | | | | | |
| **Lobianchia gemellarii* | 5 | 152 | 3 | 6 | 103,632 |
| *Lampanyctus cuprarius* | 5 | 170 | 3 | 14 | 88,233 |
| **Ceratoscopelus warmingii* | 5 | 141 | 3 | 14 | 65,986 |
| **Hygophum hygomii* | 5 | 65 | 2 | 3 | 42,394 |
| **Diaphus mollis* | 5 | 54 | 1 | 2 | 37,427 |
| **Lepidophanes gaussi* | 4 | 37 | 0 | 0 | 34,780 |
| **Hygophum reinhardtii* | 4 | 16 | 0 | 0 | 15,040 |
| **Notoscopelus resplendens* | 1 | 13 | 0 | 0 | 12,220 |
| **Lampanyctus photonotus* | 4 | 47 | 3 | 11 | 9,415 |
| **Myctophum selenops* | 2 | 9 | 0 | 0 | 8,460 |
| **Bolinichthys indicus* | 4 | 30 | 3 | 6 | 7,530 |
| **Lampanyctus lineatus* | 4 | 13 | 1 | 1 | 6,977 |
| ........ | | | | | |
| **Notoscopelus caudispinosus* | 3 | 16 | 2 | 2 | 6,405 |
| **Lobianchia dofleini* | 2 | 6 | 0 | 0 | 5,640 |
| **Group 3B** | | | | | |
| ........ | | | | | |
| **Hygophum taaningi* | 1 | 4 | 3 | 10 | 6,625 |

*Inverse ('r'-type) analysis*

The grouping of the species with inverse (or 'r'-type) analysis was only partially successful in revealing distribution pattern types. Initially all 63 species from the MT–1600 transect were included, but this led to a somewhat complex dendrogram (Fig. 15), with many species showing little similarity to others. These are either rare species, or species that are poorly represented in the R.V. *Anton Dohrn* catches. These species were then excluded from the analysis by the criterion of occurring at fewer than 10 stations and in densities of less than 6 specimens per hour per station of occurrence, as shown in Figure 16. The reduced data matrix was then reworked through the programme. The resulting dendrogram (Fig. 17) is somewhat clearer, indicating the existence of two major species groups: those found in the Temperate Region; and those found in the Subtropical Region and South Sargasso Sea Province. A similar picture of these two groupings was obtained from the IKMT data. Unfortunately, neither the dendrograms nor the ordinations allow for the recognition of the various distribution-pattern types that have been formulated in the literature. We suggest that this may be due to the fact that only the southern ranges of the temperate species and the northern ranges of the tropical and subtropical species were covered by the transects.

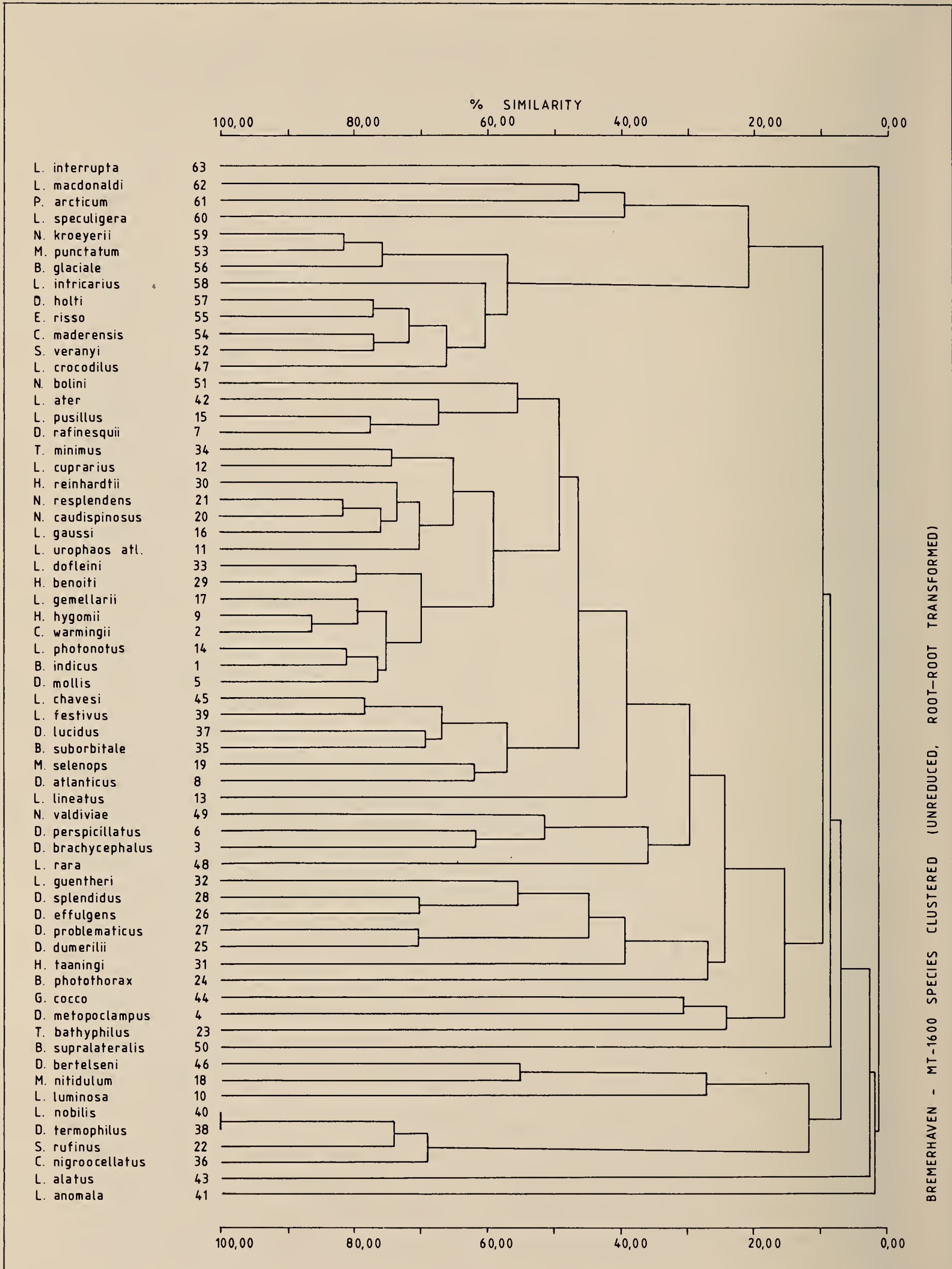


Fig. 15. Dendrogram of species affinities for 63 species from MT-1600 hauls.

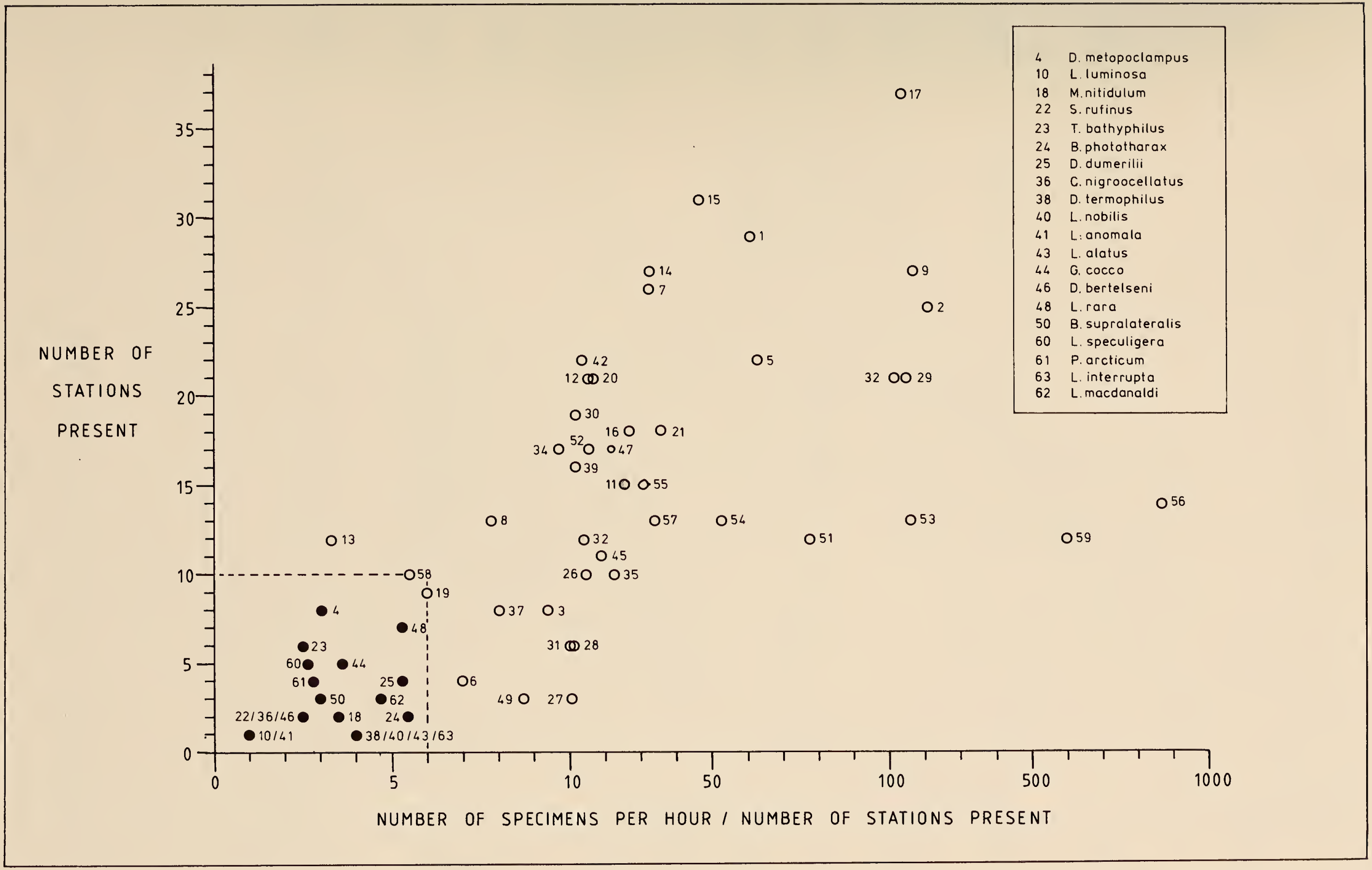


Fig. 16. Graph of the station occurrences and densities of myctophids from MT–1600 hauls. Solid circles—those species excluded from further analysis.

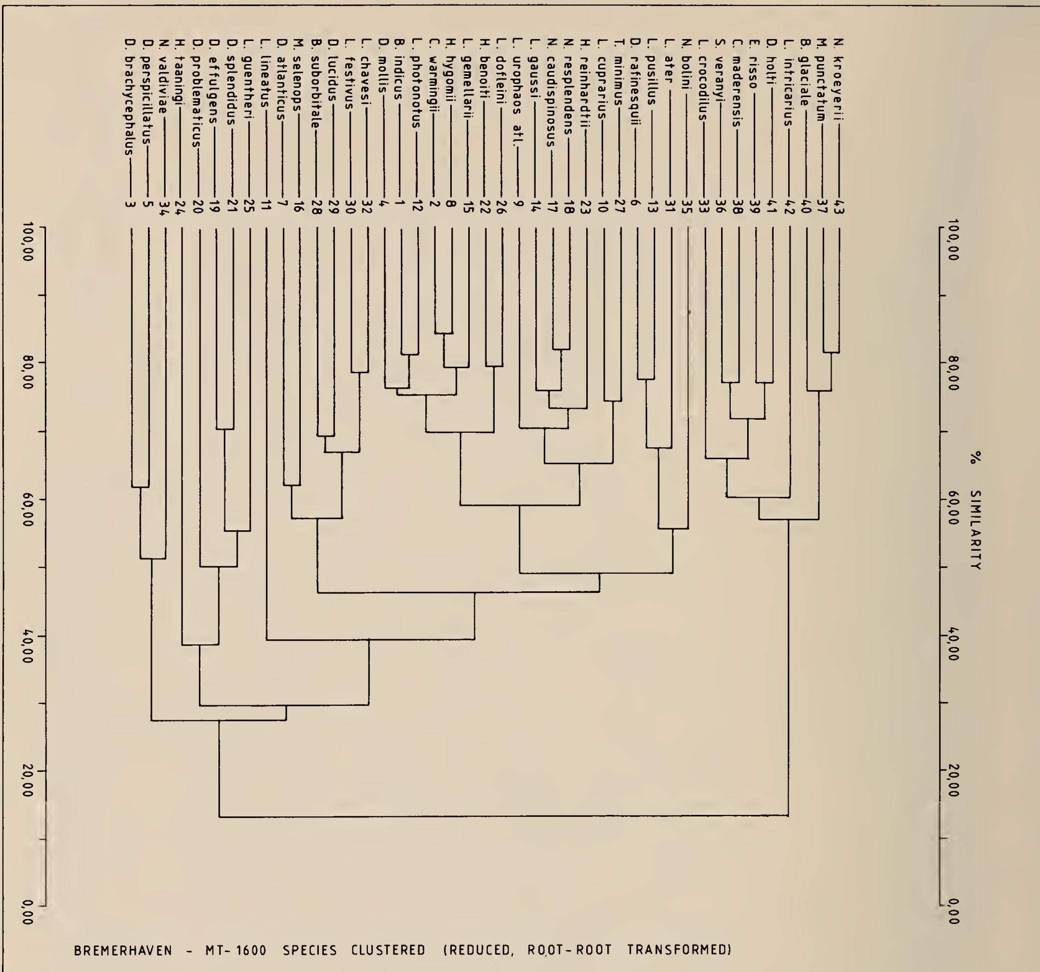


Fig. 17. Dendrogram of species affinities for reduced number of species from MT–1600 hauls.

In discussing the second and third aims of this paper (see p. 20), the distributions of *Hygophum benoiti* (characteristic of the subtropical grouping) and *Electrona risso, Benthosema glaciale*, and *Lampanyctus crocodilus* (all characteristic of the Temperate Region) are examined.

Backus *et al.* (1977) are of the opinion that *Electrona risso* (Fig. 18) is an Eastern Pattern species, which would seem to support its inclusion with the other temperate species in the context of the 1979–transects. Hulley (1981), on the other hand, suggests a relationship with the 10 °C and 15 °C isotherms at 200 m and the 50 $gCm^{-2}y^{-1}$ isoline. Except for the single larval specimen taken in a neuston tow at about 28°N 51°W, for which there is some doubt about the identification (H.-C. John, pers. comm.), the latter criteria are satisfied by the

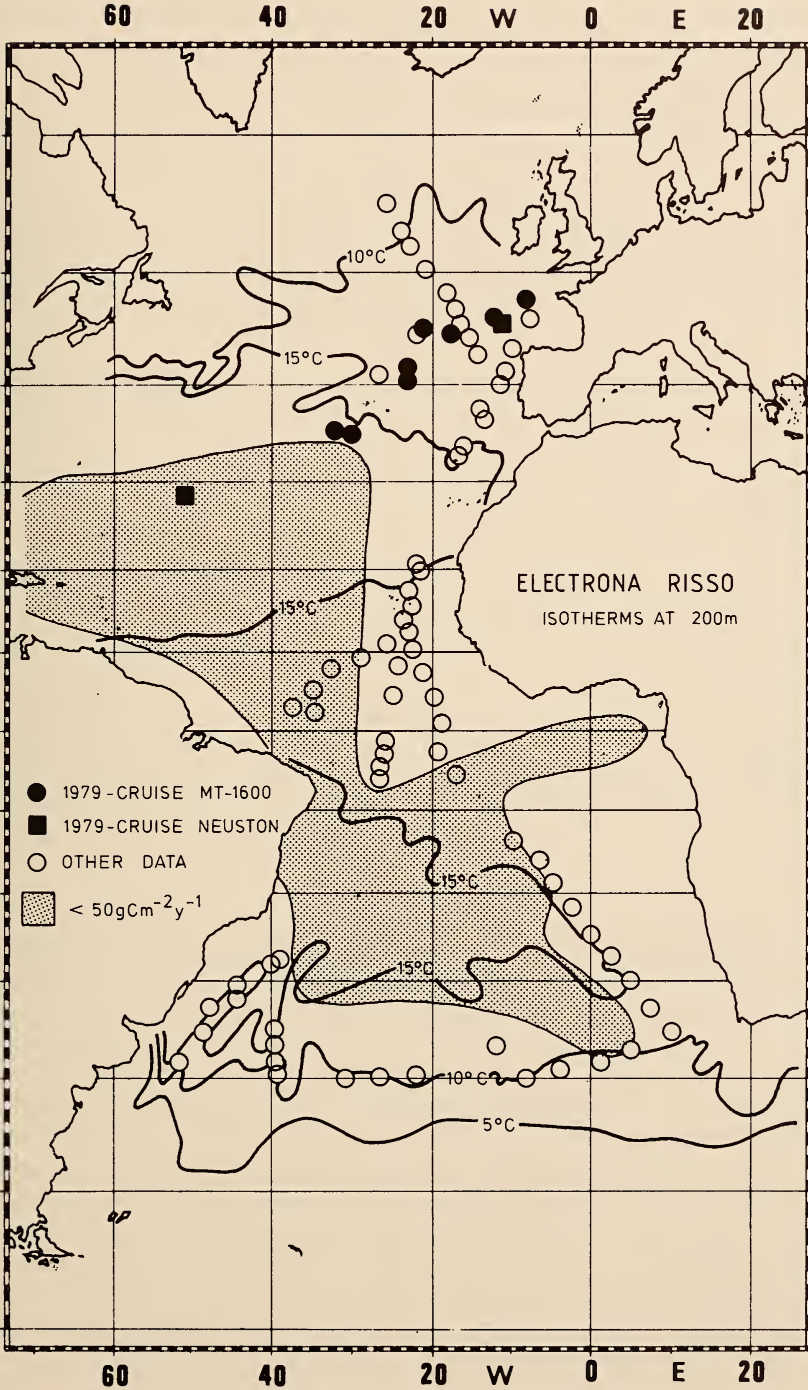


Fig. 18. Distribution of *Electrona risso*.

1979–transect data. Seen against a background of an extensive distribution, particularly in the South Atlantic (Fig. 18), *Electrona risso* should be excluded from the Eastern Pattern and be considered a widespread species within the apparent ecological constraints.

*Hygophum benoiti* has been described as a temperate-semisubtropical species by Backus *et al.* (1977), and as a temperate-subtropical species, but within the Northern Temperate Pattern, by Hulley (1981). The present transect data and indicator analyses suggest that, while *Hygophum benoiti* is indeed distributed in both temperate and subtropical regions (Fig. 19) and attains sexual maturity throughout its distributional range, it shows a closer affinity to the Subtropical

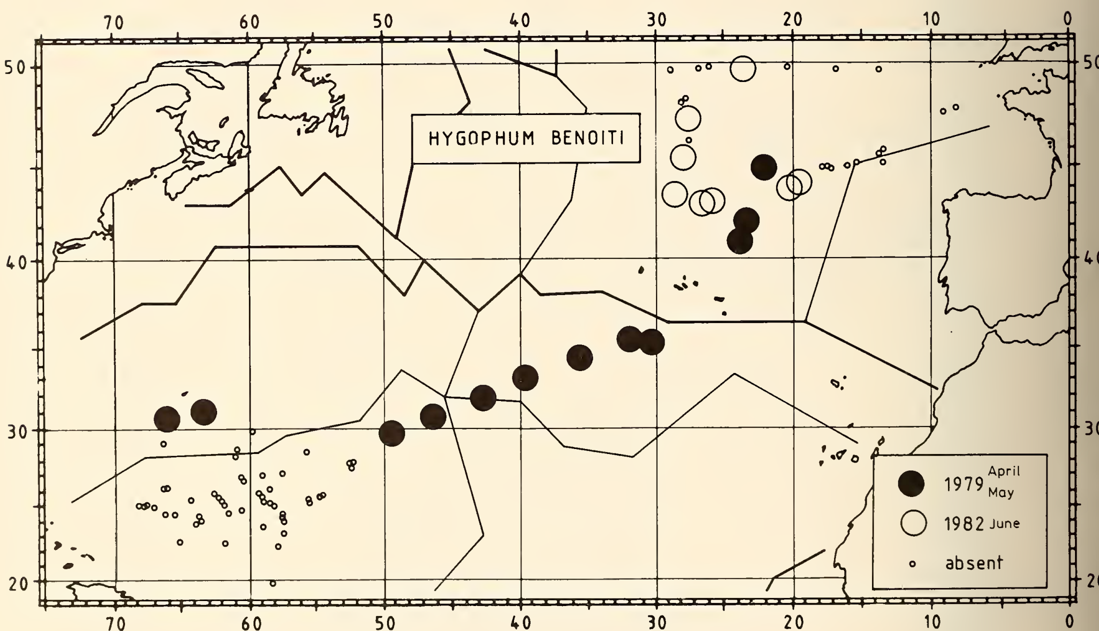


Fig. 19. Distribution of *Hygophum benoiti*.

Region than to the Temperate Region (Table 5). This suggestion was recently confirmed during the 1982–Mid-Atlantic Ridge Expedition, north of the Azores, where the species was taken in any quantity only south of about 44°S (unpublished data). This means that the distribution pattern of *H. benoiti* may be different from those of other species presently included in the Temprate-subtropical Pattern, namely *Ceratoscopelus maderensis, Diaphus rafinesquii, Notoscopelus bolini,* and *Symbolophorus veranyi.* This warrants a closer examination both of the above-mentioned temperate-subtropical species, and the species currently held under the North Subtropical Subpattern, e.g. *Lampadena urophaos atlantica*.

The distribution of *Benthosema glaciale* (Fig. 20), a shallow-living species with a night distribution between 12 m and 200 m, reveals that this Temperate Region indicator species transgresses the boundary limit, with a single specimen being taken in the northern Subtropical Region. Ordination of the MT–1600 data

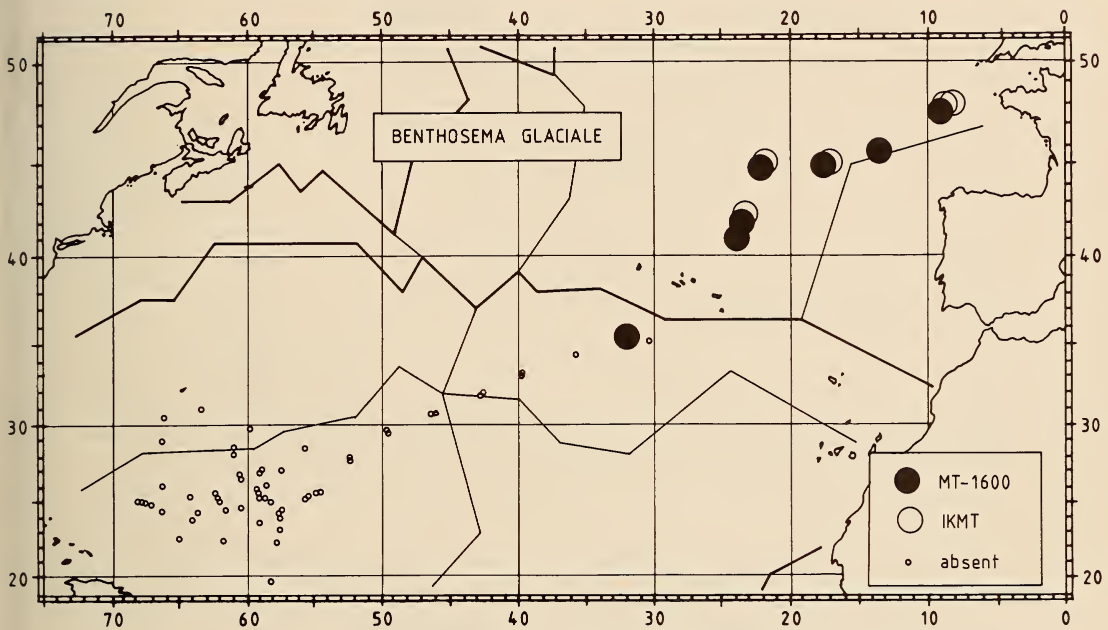


Fig. 20. Distribution of *Benthosema glaciale*.

for this species (Fig. 21) indicates that it was taken at all temperate stations, and further, that in this region there was no apparent size stratification with depth (although opening and closing nets were not employed). The specimen from the Subtropical Region is very small by comparison (Fig. 21) and may only indicate transportation of juveniles across the boundary by ocean currents. These juveniles may have no potential for achieving sexual maturity.

By contrast, *Lampanyctus crocodilus*, a somewhat deeper-living Temperate Region species, is also found to the south of the boundary between the Temperate Region and the Subtropical Region. In IKMT samples, it was taken to as far south as about 32°N, but only as small specimens (maximum SL 23 mm). The ordination (Fig. 22) reveals a marked size stratification with depth in the Temperate Region, and further, that large specimens do occur in deeper waters south of the Temperate Region boundary, to about 34°N. Since these specimens are of a potentially reproductive size (maximum SL 178 mm), future study will include the examination of changes in sexual maturity across this boundary zone.

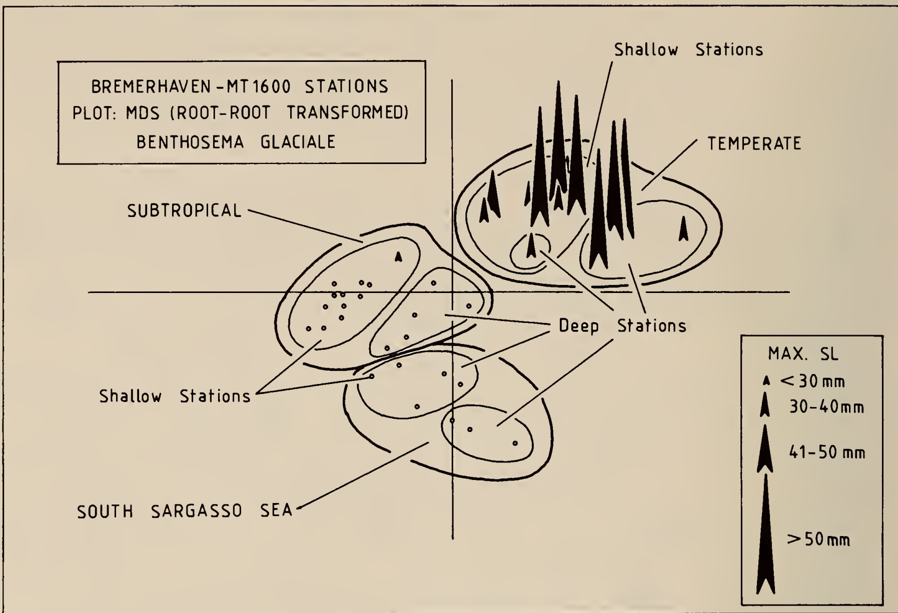


Fig. 21. MDS plot for *Benthosema glaciale* with maximum size indicated for each positive sample.

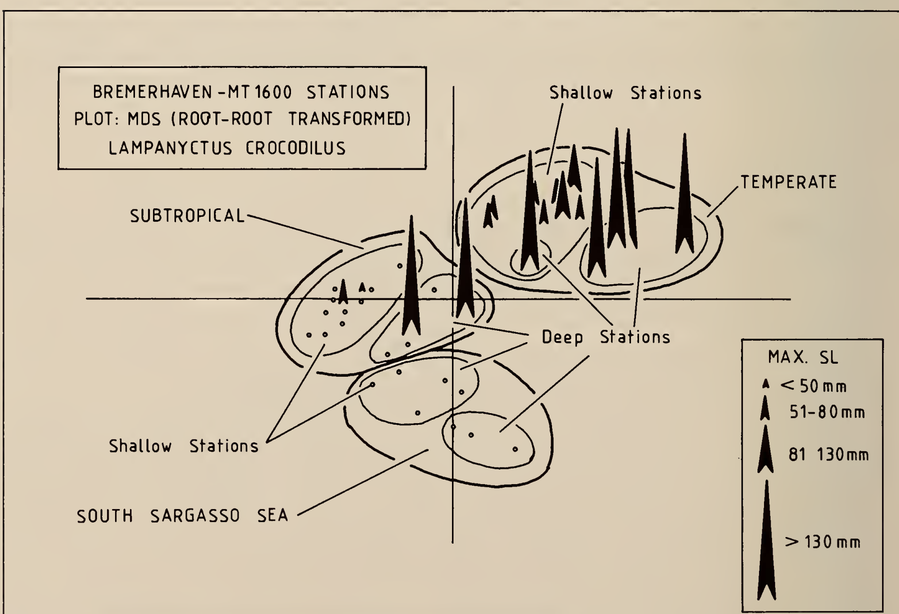


Fig. 22. MDS plot for *Lampanyctus crocodilus* with maximum size indicated for each positive sample.

A summary of the myctophid catch data from the MT–1600 transect is compared in Table 12 with the distributional patterns and subpatterns given by Hulley (1981, table 3). For a given pattern or subpattern, abundances have been calculated in mean number of specimens per hour for stations within each of the Groups 1, 2 and 3, according to the formula:

$$\text{Pattern}_j : \text{Abundance} = \frac{\sum\limits_{i(j)} \left( \sum\limits_{s(t)} n_{is} \right)}{\text{No. stations in } t}$$

where:

$n_{is}$ is the number of specimens of species '*i*' caught per hour at station '*s*';
*j* is the assembly of species within a particular distribution pattern;
*t* is the stratum of stations in each of Groups 1, 2 and 3.

However, some reservation is expressed with regard to the absolute values obtained with this gear, because of errors introduced while picking the net on deck, uncertainty of the exact time-span in which the net is actively fishing, and/or variations in the size of the mouth opening of the net.

No bathypelagic species of myctophid is endemic to the Atlantic. In the Warm Water Group of 42 species, 6 (14,3 %) are endemic to the Atlantic, while 11 (73,3 %) of the Cold Water Group of 15 species are endemic. Further, all myctophid species held under the North Temperate Pattern (Boreoarctic, Boreal, Mediterranean and Temperate-subtropical Subpatterns) in the Atlantic are endemic.

The Warm Water Group, representing 66,7 per cent of the total number of species, averaged 98 specimens per hour per station in Group 1 stations, 1 284 specimens per hour per station in Group 2 stations and 112 specimens per hour per station in Group 3 stations. Cold Water Group species, representing 23,8 per cent of the total number of species, averaged 1 862 specimens per hour per station in Group 1 stations, 202 specimens per hour per station in Group 2 stations and less than one specimen per hour per station in Group 3 stations. Widespread species, representing 6,3 per cent of the total number of species, averaged 48 specimens per hour per station, 136 specimens per hour per station, and one specimen per hour per station in Group 1, Group 2, and Group 3 stations respectively. Bathypelagic species, representing 1,6 per cent of the total number of species, averaged less than one specimen per hour per station in Group 2 and Group 3 stations and were absent in Group 1 stations.

The above confirms the general rule that species diversity decreases with increasing latitude and that larger populations occur in cold-water species than in warm-water species. Summed mean abundance values for stations in each of Groups 1, 2 and 3 give a measure of the 'standing stock' of the three areas: Group 1 (Azores–Britain Province) is 18 times more productive than Group 3 (South Sargasso Sea Province), while Group 2 (North Sargasso Sea Province–North North African Sea Province) is 14 times more productive than Group 3. In terms of oceanic myctophids, therefore, the North Atlantic Temperate Region is

TABLE 12

1979–Sargasso Sea Expedition (2nd leg). MT–1600 hauls: Comparison of myctophid specimen abundances with distributional patterns and subpatterns as given by Hulley (1981).

| | *No. of species* | *Percentage total no. of species* | *Group 1: mean no. specimens/hour* | *Group 2: mean no. specimens/hour* | *Group 3: mean no. specimens/hour* |
|---|---|---|---|---|---|
| **MESOPELAGIC** | | | | | |
| WIDESPREAD GROUP | 4 | 6,3 | 48,38 | 136,12 | 0,88 |
| Widespread Pattern | 4 | 6,3 | 48,38 | 136,12 | 0,88 |
| WARM-WATER GROUP | 42 | 66,7 | 98,46 | 1 284,18 | 111,76 |
| Tropical Pattern | 7 | 11,1 | 0,31 | 12,65 | 2,75 |
| Eurytropical Pattern | 22 | 34,9 | 23,77 | 776,53 | 64,88 |
| Subtropical Pattern | 13 | 20,6 | 74,38 | 495,00 | 44,13 |
| COLD-WATER GROUP | 15 | 23,8 | 1 862,09 | 202,24 | 0,38 |
| Bitemperate Pattern | 4 | 6,3 | 6,46 | 0,00 | 0,00 |
| Boreoarctic Subpattern | 3 | 4,8 | 1 451,62 | 0,24 | 0,00 |
| Boreal Subpattern | 2 | 3,2 | 167,85 | 0,82 | 0,00 |
| Mediterranean Subpattern | 1 | 1,6 | 30,31 | 2,71 | 0,00 |
| Temperate-subtropical Subpattern | 5 | 7,9 | 205,85 | 198,47 | 0,38 |
| **BATHYPELAGIC** | | | | | |
| WIDESPREAD GROUP | 1 | 1,6 | 0,00 | 0,59 | 0,63 |
| Widespread Pattern | 1 | 1,6 | 0,00 | 0,59 | 0,63 |
| WARM-WATER GROUP | 1 | 1,6 | 0,00 | 0,00 | 0,13 |
| Eurytropical Pattern | 1 | 1,6 | 0,00 | 0,00 | 0,13 |
| **STANDING STOCK** | | | | | |
| Summed mean abundance | | | 2 008,93 | 1 623,13 | 113,78 |
| Percentage | | | 53,63 | 43,33 | 3,04 |

1,24 times more productive than the North Atlantic Subtropical Region. Recent unpublished data from the TIFI–8 Cruise, obtained while sampling a few metres above the slope regions west of Great Britain, indicate that this value would be considerably higher if the pseudoceanic population of *Notoscopelus kroeyerii* were to be included.

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## REFERENCES

Backus, R. H., Craddock, J. E., Haedrich, R. L. & Robison, B. H. 1977. Atlantic mesopelagic zoogeography. *Mem. Sears Fdn mar. Res.* **1** (7): 266–287.

Backus, R. H., Craddock, J. E., Haedrich, R. L. & Shores, D. L. 1969. Mesopelagic fishes and thermal fronts in the western Sargasso Sea. *Mar. Biol.* **3**: 87–106.

Field, J. G., Clarke, K. R. & Warwick, R. M. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* **8**: 37–52.

Hela, I. & Laevastu, T. 1962. *Fisheries hydrography. How oceanography and meteorology can and do serve fisheries*. London: Fishing News (Books) Ltd.

Hulley, P. A. 1981. Results of the research cruises of FRV 'Walther Herwig' to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). *Arch. FischWiss.* **31** (1): 1–300.

Krefft, G. 1974. Investigations on midwater fish in the Atlantic Ocean. *Ber. dt. wiss. Kommn Meeresforsch.* **23**: 226–254.

Krefft, G. 1978. Distribution patterns of oceanic fishes in the Atlantic Ocean. *Rev. Trav. Inst. Pêches marit.* **40**: 439–460.

Nafpaktitis, B. G., Backus, R. H., Craddock, J. E., Haedrich, R. L., Robison, B. H. & Karnella, C. 1977. Family Myctophidae. *Mem. Sears Fdn mar. Res.* **1** (7): 13–265.

Parin, N. V., Andriashev, A. P., Borodulina, O. D. & Tchuvasov, V. M. 1974. Midwater fishes of the Southwestern Atlantic Ocean. *Trudy̆ Inst. Okeanol.* **98**: 76–140 (in Russian).

Wegner, G. 1979. R/V *Anton Dohrn* XBT sections in the North Atlantic Ocean between January and May 1979. *Polymode News* **70**: 3–4.

Wegner, G. 1982. Main hydrographic features of the Sargasso Sea in Spring 1979. *Helgol. Meeresunters.* **35**: 385–400.

Wüst, G. & Defant, A. 1936. Atlas zur Schichtung und Zirkulation des Atlantischen Ozeans. Schnitte und Karten von Temperatur, Salzgehalt und Dichte. *Wiss. Ergebn. dt. atlant. Exped. 'Meteor'* **6** (Atlas).